Chimpanzee (*Pan troglodytes schweinfurthii*) behavioral responses to resource scarcity in the savanna-woodland environment of Issa valley, Tanzania

Study of feeding, ranging, and grouping patterns

Camille Giuliano

Thesis submitted in partial fulfilment of the requirements of Liverpool John Moores University for the degree of Doctor of Philosophy

August 2021

Table of contents

Abstract

To survive and reproduce, primates must consume sufficient amounts of resource. Because they live in seasonal environments and mostly rely on vegetative foods, primates face temporal variations in food abundance and quality, and food shortages often have negative repercussions on their energy balance, fecundity, growth, and survival. To limit these impacts and maintain sufficient nutrient and energy intake during lean periods, primates exhibit a large range of adaptations including adjusting their diet, ranging behavior and/or group size.

Chimpanzees (*Pan troglodytes*) are one of the most studied animals but despite nearly six decades of field research, gaps remain in our knowledge of the species, particularly when it comes to communities inhabiting savanna-woodlands, the ecological edge of the species range. Savanna-woodlands differ from forests in having substantially less rainfall, which is strongly seasonal, as well as lower plant density and diversity, all of which result in resource scarcity and important fluctuations in its availability. The selective pressures operating on chimpanzees in these landscapes are thus predicted to be different than those in forests, potentially eliciting adaptations distinct from adaptations to a forested habitat, especially during times of resource (both food and water) scarcity. However, to date, we have only limited behavioral data from habituated communities in savanna-woodlands, thus restricting our ability to explore these ideas.

I investigated chimpanzee (*P. t. schweinfurthii)*, diet, ranging and grouping patterns in the savanna-woodland environment of Issa valley, Tanzania, and particularly their correlations to seasonal fluctuations in resource availability. I also compared the diet, ranging and grouping patterns observed at Issa with those of other communities. I found that, when preferred foods were scarce, Issa chimpanzees consumed young leaves from tree species growing in the open woodland habitat. In contrast to previous reports from other chimpanzee communities, during periods of low food availability Issa chimpanzees significantly increased their daily path length. Water scarcity, however, did not influence their daily path length, and neither seasonal fluctuation in food nor water availability influenced habitat use. I found that

party size at Issa was significantly influenced by seasonal variations in food but not water availability and was higher in open habitat, which is potentially characterized by a high predation risk. In general, Issa chimpanzees consumed less plant species than chimpanzees at more forested sites. Like elsewhere, they consumed mostly fruit, but other items such as leaves, flowers, and termites were also important in their annual diet probably because they provide essential proteins. Issa yearly home range was larger than most other communities for which data are available. Finally, compared to other communities, the Issa community was highly cohesive, possibly due to a combination of its small size and the potential threats (predators, neighboring communities) in their home range.

By providing data from direct observations of a chimpanzee population living in an under-studied biome, the present study brings new insights into chimpanzee behavioral responses to seasonal fluctuations in ressource availability, into the relationships between environment and behavior for this species, and into chimpanzee behavioral diversity in general. Furthermore, chimpanzee behavioral studies may be of great value to the paleoanthropological scientific community. The results of the current study could be useful to interpret archaeological records and infer extinct hominin behavior, as well as to highlight what adaptations may have set the principles for the differentiation between human and chimpanzee lineage.

Declaration

I declare that no portion of the work referred to in the thesis has been submitted in support of an application for another degree or qualification of this or any other university or other institute of learning.

Acknowledgments

This research was only possible through the help and support of incredible people. To everyone below and anyone I have accidentally omitted, thank you!

I would like first to thank my supervisors, **Alex Piel**, **Fatima Perez de Heredia** and **Antje Engelhardt** for their continuous support and guidance over the past years, which was fundamental to the success of this project. I thank them for the opportunity they have given me, and for their constant belief in my skills and abilities in conducting this research. Alex was an invaluable help, guiding me through all the stages of my PhD from field work to writing. I am also eternally grateful to him for giving me the exceptional chance to study wild chimpanzees and to live at Issa camp. I am also very grateful to my supervisor Fatima who has been extremely supportive and encouraging throughout my PhD. Particularly, her help with the nutritional part of this research has been critical to the success of my project.

I would like to thank my examiners, **Linda Marchant** and **Serge Wich** for their enthusiasm towards my work and for their very useful comments and corrections on this thesis.

I am extremely grateful to **Sylvia Ortmann** for her interest in my project, for giving me the opportunity to analyze my samples in her incredible lab and for being so welcoming. My warmest thanks also to **Heidrun Berbelen,** who analyzed all Issa food samples and was particularly patient in showing me all the stages of macronutrient analysis. She shared without reserve her fabulous lab knowledge and made so much effort to translate everything to English so that I could understand.

I am absolutely grateful to **Tobias Deschner** for his interest in my research, his extremely helpful advice and for welcoming me at MPI and into his endocrinology lab. Thank you as well to **Vera Schmeling** and **Róisín Murtagh** for guiding me and helping through the analysis of Issa chimpanzee fecal samples. Although I could not include this work in my thesis, I am thankful for this experience and for all the endocrinological expertise I gained while in Tobias' lab.

Special thanks go to **Adriana Hernandez Aguilar** for her interest in my research and for supporting macronutrient analyses. I thank as well **LJMU** for believing in my project and for providing funding for my research. I am also grateful to **COSTECH**, **TAWIRI** and the **Tanganyika District** for the permission to carry out research in Tanzania.

Furthermore, I would like to thank **Noémie Bonnin, Ineke Knot** and **Anne-Sophie Crunchant** for being such amazing roommates, inspiring women researchers and for making my stay in Liverpool so much nicer and warmer. At LJMU as well, I thank **James Waterman**, for his advice on behavioral data collection and for helping me with statistics and **Edward McLester** for guiding me through ranging data analyses.

My warmest thanks go to all the GMERC team for making me feel like home as soon as I made my first step at Issa camp, and for being my Tanzanian family for more than a year. This time at Issa was one of the best periods of my life and your wonderful company (endless card and bao games, crazy dances, evening workouts and chats by the fire) was the main part of it. I am extremely grateful to all field assistants at Issa and particularly **Mariana Marco, Simon Sungura and Kidosi Laurente** who are simply the best chimp experts and trackers one PhD student can dream to work with as well as being awesome friends. Thank you as well to all the cooks at Issa for providing me the energy to run up and down hills after chimps and for teaching me how to cook delicious chapatis! Thank you to **Allison Rogers** and **Bethan Mason** who managed everything at camp so that research could be as efficient as possible. I also thank **Anita Eriksen** for her extremely valuable help in collecting behavioral data and samples in the field. Thank you to **Yahya Abeid** for all plants identifications at Issa without whom all food availability index calculations would not have been possible. In the GMERC family I also thank **Kyle Sweeney, Daphne Vink, Seth Phillips**, **Samantha Hilty and Russel Delahunty** for being such amazing people and making my time at camp even nicer.

To all my precious friends that have accompanied me during this PhD, across 5 different countries and have been an exceptional emotional support: first, I am sorry for all the plans I canceled because of my work (!), and most importantly thank you for making my life so much nicer and funnier than just writing up a PhD, you are the best! Special thanks to **Noémie Bonnin** in UK; **Donath Nsika, Allan Ngowi, Hilder Magessa, Sianeema Makundi and Ally Mugendy Sia** in Tanzania**; Antoine Martin** in France; **Karam Skaf** in Germany; **Gaëlle Roussigné, Hawa Sidibé, Aurélie Pittet, Samuel M'gbachi Ifegwu and Mahadi Diouara** in Mali.

I thank my incredible parents, brother, and grandmother for all their love and support and more especially for trusting me and never questioning my decisions (even when it led to many sleepless nights for them as they wondered where I was and whether I was safe). You gave me one of the most beautiful presents one can get: the absolute freedom of being who I wanted to be.

I cannot describe all of the things I have to be grateful to **Josselin Noble**. You were there for every step, every up, and every down of this thesis. You gave me the strength to pursue my dream of becoming a primatologist after getting away from university and without having any experience in this field! You believed in me and pushed me to go live among primates although it implied being very far away from you. You listened to all my reflections and hesitations regarding my research and were of incredible help for someone not knowing anything about primatology! You demonstrated so much interest in my research simply because it was a part of me. You were by my side every time I doubt myself and felt insecure to remind me how much you believed in me. You were incredibly calm, patient and loving in these moments and gave me the strength to push myself farther. I am extremely lucky to have you in my life and will forever be grateful for all the joy and love you give me every single day.

List of abbreviations and notations

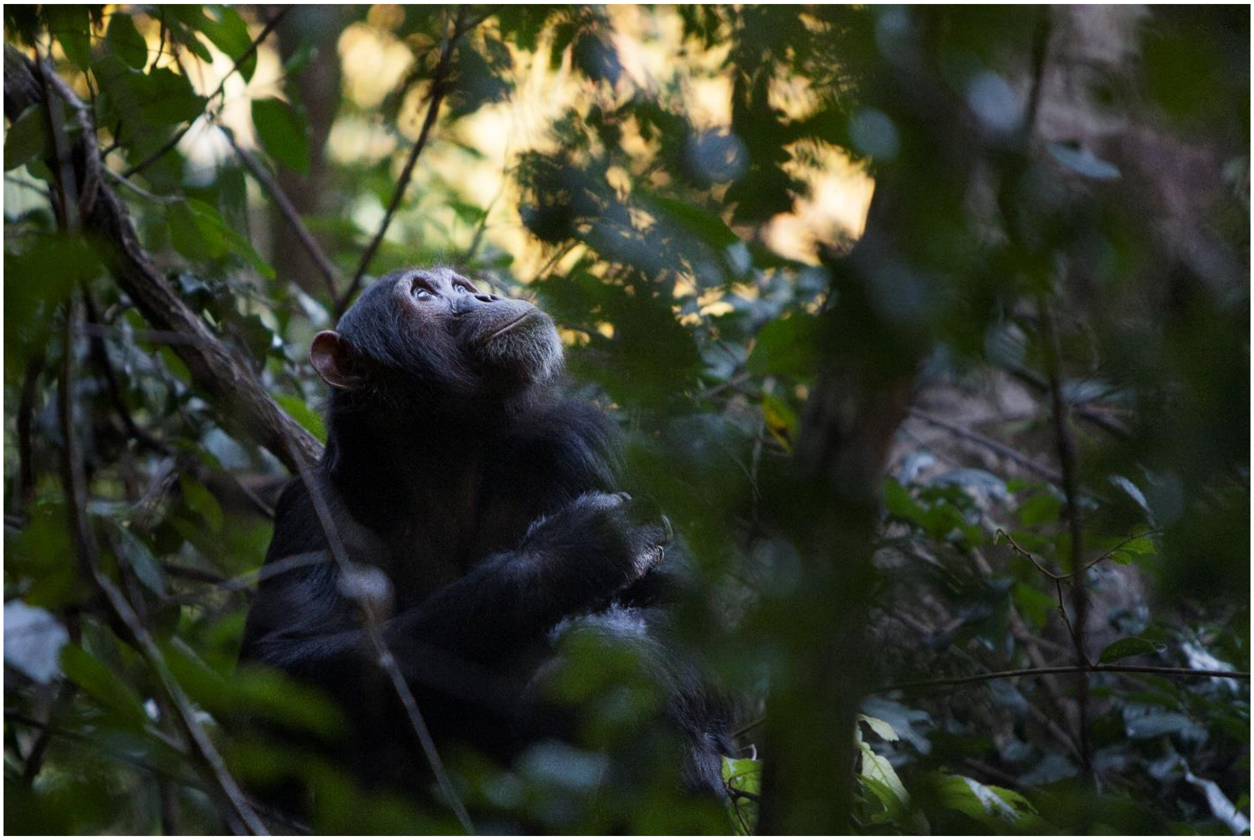
APS	Absolute party size
BA	Basal area
CAR	Central African Republic
COSTECH	Commission for science and technology
D	Density
DBH	Diameter at breast height
DNA	Deoxyribonucleic acid
DPL	Daily path length
DRC	Democratic Republic of Congo
E	Energy
FA	Food availability
FAIe	Food availability index
FBF	Fallback food
GC	Grid cell
GLM	Generalized linear model
GLMM	Generalized linear mixed model
GMERC	Greater Mahale ecosystem research and conservation
HR	Home range
IZW	Institute for Zoo and Wildlife research, Berlin
LJMU	Liverpool John Moores University
M	Mass
MCP	Minimum convex polygon
MN	Macronutrient
MPI	Max Planck Institute
n	Sample size
NS	Non-significant
PFAIe	Preferred food availability index
RPI	Rank preference index

RPS	Relative party size
SD	Standard deviation
SE	Standard error
sp.	Species
spp.	Several species
SW	Savanna-woodland
TAWIRI	Tanzanian wildlife research institute
THV	Terrestrial herbaceous vegetation
USO	Underground storage organ
WAI	Water availability index

List of figures

List of tables

Chapter 1: General introduction



1. Seasonality and variation in food availability in primates

Seasonality refers to recurrent climatic fluctuations that tend to have a period of one year and that are likely to have an impact on the phenology of the plant community, and thus on the abundance, nature, and distribution of potential food items (van Schaik and Brockman, 2005). Contrary to some other vertebrate species, primates do not undertake long seasonal migrations nor hibernate (except for some small strepsirrhines species: Blanco *et al.*, 2018) to avoid lean periods. Instead, most of their responses to reduced resource availability are behavioral with, for instance, adjustments in their feeding, ranging and grouping strategies (van Schaik *et al.*, 1993). As food become scarce, primates may continue to obtain an adequate amount of energy and nutrients by either, increasing their daily travel distance to visit more patches, or by switching to abundant foods that may be of lower quality but require less travel such as leaves, unripe fruits, *etc.* (Stephens and Krebs, 1986; Hemingway and Bynum, 2005). Primates may also switch area and move into a phenologically different habitat, where food is temporally more abundant (Stevenson *et al.*, 1994; Defler, 1996; Poulson *et al.*, 2001). This can occur within populations that live in heterogenous landscapes, such as mountain slopes, savanna-woodland mosaics, flood-plains and uplands, valleys and hillsides, *etc.* (van Schaik and Brockman, 2005). Individuals have thus the opportunity to move into different types of habitats, with varying sun exposure, slope, soil chemistry, moisture, *etc.*, which creates strongly varying constraints on plant growth, resulting in heterogeneous phenological patterns (Duvall, 2011). Responses to fluctuations in food abundance may also be social, particularly in species characterized by a fission-fusion social system (Doran, 1997; Aureli *et al.*, 2008). The term fission-fusion describe populations where subgroup size varies and notably where individuals split into small parties when food is scarce as a way of reducing feeding competition (Aureli *et al.*, 2008).

All primate habitats show seasonal variations in their food availability and are characterized by periods of food scarcity, but the frequency, severity, and duration of scarcity vary greatly from site to site, and the associated consequences on consumers are likely to vary accordingly (van Schaik *et al.*, 1993). More than the average environmental conditions, it is the intensity of the variations, and particularly the severity of the resource-scarce periods, that shape individual behavioral ecology, because it is often the ability to go through these periods that will determine individual survival (Brockman, 2005). Extreme seasonality in some primate environments has presumably selected for a wide range of behavioral adaptations that confer the flexibility needed to survive to severe and prolonged periods of resource scarcity (Lefebvre *et al.*, 2004). For instance, a recent study comparing the behavior of chimpanzee (*Pan troglodytes*) at 144 locations demonstrated that seasonal and unstable environmental conditions are associated with greater within-species behavioral diversity (Kalan *et al.*, 2020). As such, behavioral plasticity seems to be a key adaptive strategy for chimpanzees and other primates living in highly seasonal environments.

2. Chimpanzee behavioral ecology

Chimpanzees are ideal candidates to study behavioral plasticity in response to environmental variability because they live across a wide range of habitats and, with a geographic range of more than 2.6 million km², they have the widest distribution among all great apes (Humle *et al.*, 2016). To date, four chimpanzee subspecies are recognized: (1) *P. t. verus* that ranges from southeastern Senegal and southwestern Mali towards southern Guinea-Bissau, Sierra Leone, Guinea, Liberia, Ivory Coast, and Ghana; (2) *P. t. ellioti* found only in Nigeria and Cameroon; (3) *P. t. troglodytes* in central Africa, extending from southern Cameroon and western Central African Republic (CAR) into Equatorial Guinea, Gabon and the extreme west of the Democratic Republic of Congo (DRC); and (4) *P. t. schweinfurthii* that ranges from the east of the CAR, the north and east of the DRC, western Uganda, Rwanda, Burundi, and western Tanzania with a small, relict population in South Sudan (Humle *et al.*, 2016) (see Figure 1.1).

Chimpanzees are one of the most studied animals (Bezanson and Mcnamara, 2019). Research on captive chimpanzees began in the 1920s, and the first studies in the wild started only in the 1960s with Goodall and Nishida's work at Gombe and Mahale, respectively, along the eastern shore of Lake Tanganyika in Tanzania (Goodall, 1986; Nishida, 2012). Goodall's mentor, Louis Leakey, hoped that studying wild chimpanzees would provide essential context for understanding human evolution (Leakey, 1970). At both sites, chimpanzees could first be approached by provisioning, and the individuals became progressively habituated to the researchers’ presence, which allowed researchers to follow and collect detailed behavioral data on wild individuals for the first time. From this method emerged some pioneering findings on chimpanzee behavior, such as tool use (Goodall, 1970), group hunting, meat sharing (Goodall, 1968), the fission-fusion social system (Nishida, 1968) and hostile intergroup relations (Goodall, 1986). Research at Mahale and Gombe is ongoing today (Nakamura *et al.*, 2013; Wilson, 2021), while additional long-term research sites have been initiated in many other countries including at Fongoli, Senegal (*e.g.*, Pruetz, 2021), Assirik, Senegal (*e.g.*, Hunt and McGrew, 2002), Taï, Ivory Coast (*e.g.*, Wittig, 2018), Bossou, Guinea (*e.g.*, Bryson-Morrison *et al.*, 2017), Loango, Gabon (*e.g.*, Martínez *et al.*, 2021), Nyungwe, Rwanda (*e.g.*, Moore *et al.*, 2018), Kibale, Uganda (*e.g.*, Emery Thompson *et al.*, 2020), Ngogo, Uganda (*e.g.*, Potts *et al.*, 2016), Budongo, Uganda (*e.g.*, Reynolds, 2006), and now Issa, Tanzania (*e.g.*, Piel *et al.*, 2017).

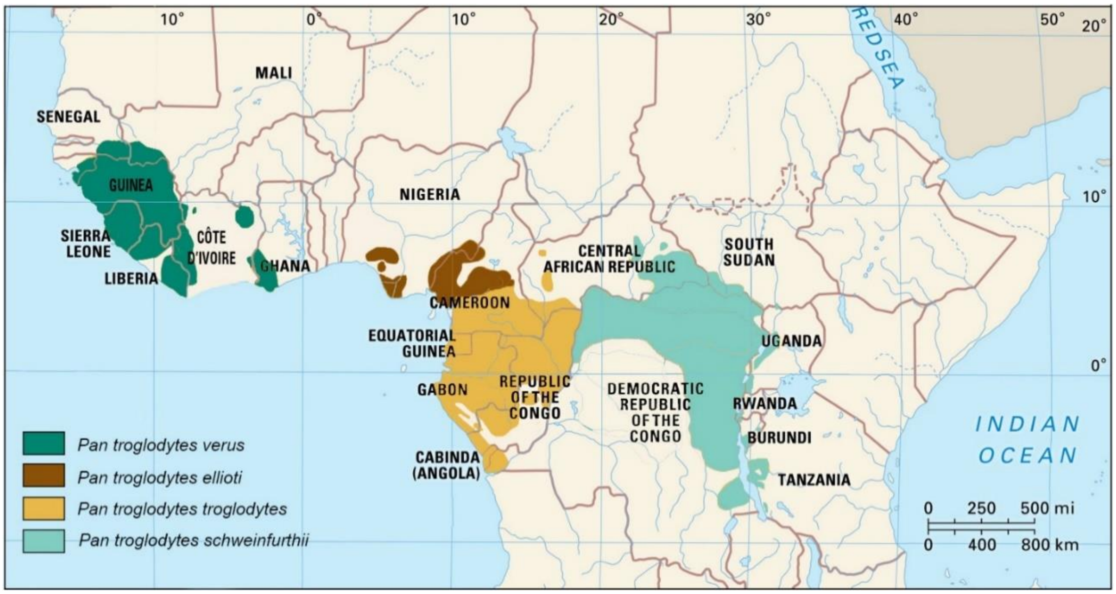


Figure 1.1 Chimpanzee (*Pan troglodytes*) geographical distribution according to subspecies. Source: Humle *et al.*, (2016)

Chimpanzee behavioral ecology is regularly monitored at these sites. We now know from these studies that chimpanzees are a highly social species living in multi-male, multi-female communities of about 20 to 150 individuals where members fission and fuse to form temporary parties that regularly change in size and composition (Lehmann and Boesch, 2004). They are long-lived, sometimes reaching 40–50 years old in the wild (Thompson *et al.*, 2007). Male chimpanzees are philopatric and typically much more gregarious than females are (Wrangham, 2000). Males compete aggressively for dominance status within the community and can sometimes form coalitions and long-term alliances to achieve or maintain their status (Nishida, 1983). Males also defend their territories vigorously against neighbors by actively patrolling the boundaries of their territory and occasionally making aggressive (and sometime lethal) incursions into neighboring communities (Watts and Mitani, 2001). Female chimpanzees generally disperse from their natal groups after reaching sexual maturity (Boesch and Boesch-Achermann, 2000) and begin to reproduce at an average age of 14 with an interbirth interval of approximately 5–6 years (Wallis, 1997). Chimpanzees feed principally on ripe fruits but also consume different plant parts, insects, and vertebrate prey (Wrangham, 1977) and range over large territories to meet their high nutritional demands (Harvey and Clutton-Brock, 1981). They are known to use tools, often to acquire foods that are difficult to obtain such as termites and hard nuts (McGrew, 2010). Chimpanzees are also extraordinarily successful predators that sometimes share meat between the community members (Boesch, 2002). All these data, gathered from various communities, provide essential information on wild chimpanzee behavioral ecology. However, while chimpanzees live across a wide range of habitats, from rainforest to savanna-woodlands (van Leeuwen *et al.*, 2020), most of the data gathered on wild chimpanzees come from populations inhabiting the forested edge of the habitat spectrum (*e.g.*, Goodall, 1986; Boesch and Boesch-Achermann, 2000; Nakamura *et al.*, 2013), thus restricting our capacity to appreciate the species behavioral diversity (Kalan *et al.*, 2020).

3. Savanna-woodlands as current habitats for chimpanzees

All four chimpanzee subspecies are found in open and dry savanna-woodlands (Marchant *et al.*, 2020; van Leeuwen *et al.*, 2020; Lindshield *et al.*, 2021). Chimpanzees living in savanna-woodlands are often called 'savanna chimpanzees', 'dry-habitat chimpanzees', or 'savanna-dwellers' (*e.g.*, McGrew *et al.*, 1981; Moore, 1992; Russak, 2013). Kortlandt (1983) identified four savanna-woodland regions within the chimpanzee distribution: (1) a zone covering southeastern Senegal, southwestern Mali and northern Guinea; (2) an isolated site in the northwestern CAR; (3) a zone stretching from eastern CAR to southwestern South Sudan; and (4) a zone approximately 100 km east of the Lake Tanganyika in Tanzania.

Although there is no consensus in the terminology, the term "savanna" usually refers to a landscape characterized by a layer of dispersed deciduous trees with a grassy understory and only a minimal amount of evergreen forest cover (Bourliere and Hadley, 1983). While landscape structure may vary between savanna-woodland sites, and chimpanzee habitats should be considered as a continuum, areas defined as savannas are usually drier than forested sites (Lindshield *et al.*, 2021), with a mean annual rainfall of less than 1360 mm and longer dry seasons (*i.e.*, > 6 months) (van Leeuwen *et al.*, 2020). Savanna-woodlands are also generally more resource-scarce and much more seasonal than forest landscapes (Moore, 1996; Hunt and McGrew, 2002; Lindshield *et al.,* 2021).

The selective pressures operating on chimpanzees in these landscapes are thus predicted to be different, potentially eliciting adaptations distinct from those to a forested habitat (Kalan *et al.*, 2020). Detailed comparative studies of chimpanzees living in varied habitats, from rainforest to savanna-woodland, reveal that some behavioral patterns are universal (*e.g.*, shelter construction, fission-fusion social system), while others seem to be associated with the 'savanna-woodland life', such as tool-assisted hunting (Pruetz *et al.*, 2015), cave use (Pruetz, 2007), extractive foraging (Hernandez-Aguilar *et al.*, 2007), or pool use (Pruetz and Bertolani, 2009). Compared with chimpanzee populations living in more closed and/or wetter habitats, chimpanzees in savanna-woodlands studied so far have been thought to generally have a narrower diet, to consume larger amounts of invertebrates (Moore, 1992; Pruetz, 2006) and to have larger home ranges (Baldwin *et al.*, 1982). However, still relatively little is known on chimpanzees living in savanna-woodlands (Marchant *et al.*, 2020; Lindshield *et al.*, 2021), and we generally lack detailed behavioral data from individuals habituated to human presence in these landscape (Lindshield et al., 2021; but see work at Fongoli: *e.g.,* Pruetz, 2006; Pruetz, 2007, Pruetz *et al.*, 2015, Pruetz and Bertolani, 2009) to get a broader picture of the species behavioral diversity .

4. Chimpanzees as referential models for early hominins behavior

As well as informing on the species behavioral diversity, studies of chimpanzees in different contexts have the potential to shed light on human evolution. In 'The Origin of Species', Darwin (1859) laid the foundation for an evolutionary understanding of human origins, and researchers such as Huxley, and later Leakey, hypothesized that human evolution was closely tied to apes' evolution (Huxley, 1863; Leakey, 1970); however, the precise evolutionary relationships between these species has been elucidated only recently. Along with the other great apes (*i.e.*, gorillas: *Gorilla* spp., bonobos: *Pan paniscus*, and orangutans: *Pongo* spp.), chimpanzees and humans (modern and extinct) form the Hominidae family, also referred to as hominids (Fleagle, 2013). In 2005, when the chimpanzee genome was sequenced, we learnt that we share about 99% of our DNA with chimpanzees (Cheng *et al.*, 2005), making them – together with bonobos – hominin's closest living relative. Hominins include both modern humans, as well as their extinct relatives such as species from the genus *Sahelanthropus*, *Orrorin*, *Ardipithecus*, *Kenyanthropus*, *Australopithecus*, *Paranthropus* and *Homo* (Fleagle, 2013). When mentioning early hominins, researchers refer to earliest members of the human lineage such as *Sahelanthropus, Orrorin, Ardipithecus* and early *Australopithecus*. The divergence between hominins and chimpanzees has been estimated to happen approximately 6.5–7.5 million years ago (Muller *et al.*, 2017). This phylogenetic proximity led some researchers to suggest that chimpanzees could provide a window into some aspects of our extinct ancestors (reviewed in Muller *et al.*, 2017), although others highlighted that non-chimpanzee primate species are also relevant in the context of human evolution (Sayers and Lovejoy, 2008).

One of the most difficult challenges in the study of human origins is the reconstruction of early hominin behavior (Plavcan, 2013), because unlike skeletal remains, behavior does not fossilize. Researchers have sought to infer early hominin life based on behavioral similarities and differences between chimpanzees and humans (fossils and extant) (Mitani, 2013). The process of using chimpanzees as models for behavioral reconstructions of early hominin behavior is called ‘referential modelling’ (Mitani, 2013) and typically involves collecting detailed information on the behavior of living chimpanzees. For instance, after observing female chimpanzees making and using tools to fish termites more frequently than males, McGrew (1979) drew parallels between chimpanzee sex differences in foraging and the division of labor that exists in hunter–gatherer societies. Stanford (1995) used data on the hunting behavior of chimpanzees to make inferences about early hominins’ hunting tactics. Based on male chimpanzee behavior, Foley (1989) hypothesized that strong kin bonds among males characterized the behavior of the last common ancestor between humans and chimpanzees. Lethal intergroup aggression is also thought to have characterize the behavior of the common ancestor because both species share this behavioral trait (Wrangham and Peterson, 1996). Chimpanzee diet composition may affect how we understand paleo-isotopic records (Sponheimer *et al.*, 2006), and analyses of chimpanzee positional behavior could influence how we interpret early hominin pelvic remains and consequently how we reconstruct their bipedal walking proficiency (Thompson *et al.*, 2015). Altogether, chimpanzee behavioral studies are useful to infer extinct hominin behavior, to draw hypotheses of our species’ evolutionary origins and to interpret paleontological and archaeological records.

5. The role of savanna-woodlands and seasonality in human evolution

Studies of chimpanzees living in savanna-woodlands, in particular, have the potential to provide important data for modeling early hominin behavior and adaptations (Suzuki, 1969; Kano, 1971; Itani, 1979; McGrew *et al.*, 1981; Baldwin *et al.*, 1982; Sept, 1992; Moore, 1996). Climate and vegetation patterns of current savanna-woodland chimpanzee sites are very similar to those reconstructed for many early hominin sites (Reed, 1997; Schoeninger *et al.*, 2003). Many scenarios describe the ecological change that occurred during the late Pliocene (~3.0 Ma) in the form of a gradual shift from forest to savanna-woodland habitat and how that may have led to the evolution of some of the key adaptations that distinguish humans from chimpanzees (Reed, 1997; Potts, 1998; White *et al.*, 2009; Domínguez-Rodrigo, 2014; Robinson *et al.*, 2017). Establishing the extent to which these changes in environmental conditions could have selected for hominin adaptations is of primary interest (Antón *et al.*, 2014).

Compared to the closed, more homogeneous forests, these open savanna-woodlands were drier (Bromage and Schrenk, 1995; Potts, 1998; Cerling *et al.*, 2011), less abundant in food sources (Isbell and Young, 1996) and more seasonal (Foley, 1993). The more dispersed and patchy plant resources are likely to have selected for longer day ranges, for instance, which in turn could have played a major role in the selection for bipedalism (Isbell and Young, 1996). Furthermore, patchier environments are likely to have promoted a greater degree of fissioning behavior in feeding parties, which may have been one of the bases for later human complex social structure (Foley, 2001). Additionally, several authors have suggested that the success of hominins may have been linked to some behavioral innovations in response to the severe temporal food shortages in the highly seasonal savanna-woodlands (Hatley and Kappelman, 1980; Wrangham *et al.*, 1999; Conklin-Brittain *et al.*, 2002). Early hominins may have been able to seasonally modify their dietary patterns, including perhaps switching to more diverse vegetative diets, and developing innovative ways of acquiring alternative or novel foods (*e.g.*, tool making) such as underground storage organs and meat (Ungar and Sponheimer, 2011). These possible dietary adjustments in response to food scarcity are reflected in archeological records with changes in dentition and jaw morphology (Grine *et al.*, 2012), and are also supposed to have allowed for increased manual dexterity, body size and encephalization (Foley, 1993; Knott, 2005; Boyd and Silk, 2012). The development of innovative ways of tracking and acquiring alternative or novel foods may have thus been a key behavioral innovation that contributed to the success of the hominin lineage and the human-chimpanzee differentiation. As behavioral reconstructions remain a real challenge in the study of extinct species, interpretations about how early hominins would have responded to these drier, more open and seasonal environment are difficult (Mitani, 2013; Plavcan, 2013). Examination of how increased seasonality and resource scarcity affect extant chimpanzees living in savanna-woodlands has the potential to facilitate our reconstructions of the challenges that hominids were facing during the Plio-Pleistocene, as well as providing new hypotheses into how early hominins could have responded to these constraints, or else highlighting what selection pressures may have set the principles for the differentiation between human and chimpanzee lineage.

6. Thesis aim, research questions

Despite nearly six decades of field research, gaps remain in our understanding of chimpanzees, particularly when it comes to communities inhabiting savanna-woodlands (Marchant *et al.*, 2020; Lindshield *et al.*, 2021). By focusing on wetter, more forested habitats, we miss key behavioral diversity only exhibited under certain environments that in turn, impairs our broader understanding of the species (Kalan *et al.*, 2020). Research on the behavioral ecology of savanna-woodland chimpanzees has numerous implications, such as redressing profound and longstanding views of chimpanzee by revealing how adaptable and flexible the species can be in its ecology and yielding important insights into hominin evolution. By studying chimpanzee diet, grouping, and ranging patterns on a newly habituated community in the savanna-woodland landscape of Issa valley, I will help determine how chimpanzees adapt their behavioral ecology to environmental characteristics of this ecosystem and specifically to seasonal fluctuations in resource availability.

I sought to address four main questions with this research:

(1) How do Issa chimpanzees adapt their diet to temporal fluctuations in food availability and particularly, what is their dietary strategy to face periods of preferred food scarcity? (Chapter 3)

(2) How do fluctuations in resources availability (food and water) shape Issa chimpanzee home range, daily traveled distance and habitat use? (Chapter 4)

(3) Do Issa chimpanzees modify their grouping patterns according to resource availability and what other factors shape party size at Issa? (Chapter 5)

(4) How do diet, ranging, and grouping patterns at Issa compare to what is found at other sites? (Chapter 3, 4 and 5)

7. Thesis outline

This chapter (**Chapter 1**) has introduced chimpanzee behavioral ecology and its relevance in understanding human evolution, with a specific focus on savanna-woodlands populations. It has highlighted the particularities of savanna-woodlands and emphasized why it is crucial to get behavioral data from chimpanzee populations living in these landscapes. I also outlined the thesis aim and research questions.

Chapter 2 provides specific details of the study site, study subjects, the general methods of data collection, and describe Issa environmental data (climate and resource availability) during the study period.

Chapter 3 analyzes Issa chimpanzees' diet, their important, preferred, and fallback foods and the temporal changes in diet throughout the study period.

Chapter 4 explores Issa chimpanzees' ranging patterns and habitat use, and how fluctuations in resources availability influence them.

Chapter 5 investigates Issa chimpanzees' party size, its socio-environmental influences, and its temporal fluctuations.

Chapter 6 provides a summary of the thesis, in which I combine and discuss the main findings.

8. References

Antón, S.C., Potts, R., Aiello, L.C., 2014. Evolution of early Homo : An integrated biological perspective. Science. 345, 45–59.

Aureli, F., Schaffner, C.M., Boesch, C., Bearder, S.K., Call, J., Chapman, C.A., Connor, R., Fiore, A.D., Dunbar, R.I.M., Henzi, S.P., Holekamp, K., Korstjens, A.H., Layton, R., Lee, P., Lehmann, J., Manson, J.H., Ramos-Fernandez, G., Strier, K.B., Schaik, C.P. van, 2008. Fission-fusion dynamics. Current Anthropology. 49, 627–654.

Baldwin, P.J., McGrew, W.C., Tutin, C.E.G., 1982. Wide-ranging chimpanzees at Mt. Assirik, Senegal. International Journal of Primatology. 3, 367–385.

Bezanson, M., Mcnamara, A., 2019. The what and where of primate field research may be failing primate conservation. Evolutionary Anthropology. 28, 166–178.

Blanco, M.B., Dausmann, K.H., Faherty, S.L., Yoder, A.D., 2018. Tropical heterothermy is “cool”: The expression of daily torpor and hibernation in primates. Evolutionary Anthropology. 27, 1–15.

Boesch, C., 2002. Cooperative hunting roles among Taï chimpanzees. Human Nature. 13, 27–46.

Boesch, C., Boesch-Achermann, H., 2000. The Chimpanzees of the Taï Forest: Behavioural Ecology and Evolution. Oxford University Press, Oxford.

Bourliere, F., Hadley, M., 1983. Present-day savannas: an overview. In: Bourliere, F. (Ed.), Ecosystems of the World, 13, Tropical Savannas. Elsevier Scientific, Amsterdam, pp. 1–17.

Boyd, R., Silk, J.B., 2012. How Humans Evolved. Sixth edition. Norton & Company, New York.

Brockman, D.K., 2005. What do studies of seasonality in primates tell us about human evolution? In: Brockman, D K, van Schaik, C.P. (Eds.), Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates. Cambridge University Press, Cambridge, pp. 543–570.

Bromage, T.G., Schrenk, F., 1995. Biogreographic and climatic basis for a narrative of early hominin evolution. Journal of Human Evolution. 28, 109–114.

Bryson-Morrison, N., Tzanopoulos, J., Matsuzawa, T., Humle, T., 2017. Activity and habitat use of chimpanzees (*Pan troglodytes verus*) in the anthropogenic landscape of Bossou, Guinea, West

Africa. International Journal of Primatology. 38, 282–302.

Cerling, T.E., Wynn, J.G., Andanje, S.A., Bird, M.I., Korir, D.K., Levin, N.E., Mace, W., Macharia, A.N., Quade, J., Remien, C.H., 2011. Woody cover and hominin environments in the past 6 million years. Nature. 476, 51–56.

Cheng, Z., Ventura, M., She, X., Khaitovich, P., Graves, T., Osoegawa, K., Church, D., DeJong, P., Wilson, R.K., Pääbo, S., Rocchi, M., Eichler, E.E., 2005. A genome-wide comparison of recent chimpanzee and human segmental duplications. Nature. 437, 88–93.

Conklin-Brittain, N.L., Wrangham, R.W., Smith, C.C., 2002. A two-stage model ofincreased dietary quality in early hominid evolution: the role of fiber. In: Ungar, P.S., Teaford, M.F. (Eds.), Human Diet: Its Origin and Evolution. Bergin and Garvey, Westport, pp. 61–76.

Darwin, C., 1859. On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. John Murray, London.

Defler, T.R., 1996. Aspects of the ranging pattern in a group of wild woolly monkeys (*Lagothrix lagotricha*). American Journal of Primatology. 38, 289–302.

Domínguez-Rodrigo, M., 2014. Is the "'savanna hypothesis'" a dead concept for explaining the emergence of the earliest hominins ? Current Anthropology. 55, 59–81.

Doran, D., 1997. Influence of seasonality on activity patterns, feeding behavior, ranging, and grouping patterns in Taï chimpanzees. International Journal of Primatology. 18, 183–206.

Duvall, C.S., 2011. Biocomplexity from the ground Up: Vegetation patterns in a West African savanna landscape. Annals of the Association of American Geographers. 101, 497–522.

Emery Thompson, M., Muller, M.N., Machanda, Z.P., Otali, E., Wrangham, R.W., 2020. The Kibale Chimpanzee Project : Over thirty years of research, conservation, and change. Biological Conservation. 252, 1–13.

Fleagle, J.G., 2013. Primate Adaptation and Evolution. Academic Press, San Diego.

Foley, R.A., 1989. The evolution of hominid social behaviour. In: Standen, V., Foley, R.A. (Eds.), Comparative Socioecology: The Behavioural Ecology of Humans and Other Mammals. Blackwell

Scientific Publications, Oxford, pp. 473–494.

Foley, R.A., 1993. The influence of seasonality on hominid evolution. In: Ulijaszek, S.J., Strickland, S.S. (Eds.), Seasonality and Human Ecology: 35th Symposium Volume of the Society for the Study of Human Biology. Cambridge University Press, Cambridge, pp. 17–37.

Foley, R.A., 2001. Evolutionary perspectives on the origins of human social institutions. Proceedings of the British Academy. 110, 171–195.

Goodall, J., 1968. The behaviour of free-living chimpanzees in the Gombe stream reserve. Animal Behaviour Monographs. 1, 161–311.

Goodall, J., 1970. Tool-using primates and other vertebrates. In: Lehrman, D.S., Hinde, R.A., Shaw, E. (Eds.), Advances in the Study of Behavior, Volume 3. Academic Press, New York, pp. 195–249.

Goodall, J., 1986. The Chimpanzees of Gombe: Patterns of Behavior. The Belknap Press of Harvard University Press, Cambridge.

Grine, F.E., Sponheimer, M., Ungar, P.S., Lee-thorp, J., Teaford, M.F., 2012. Dental microwear and stable isotopes inform the paleoecology of extinct hominins. American Journal of Physical Anthropology. 317, 285–317.

Harvey, P.H., Clutton-Brock, T.H., 1981. Primate home-range size and metabolic needs. Behavioral Ecology and Sociobiology. 8, 151–155.

Hatley, T., Kappelman, J., 1980. Bears, pigs, and Plio-Pleistocene hominids: a case for the exploitation of below ground food resources. Human Ecology. 8, 371–387.

Hemingway, C.A., Bynum, N., 2005. The influence of seasonality on primate diet and ranging. In: Brockman, D.K., van Schaik, C.P. (Eds.), Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates. Cambridge University Press, Cambridge, pp. 57–104.

Hernandez-Aguilar, R.A., Moore, J., Pickering, T.R., 2007. Savanna chimpanzees use tools to harvest the underground storage organs of plants. Proceedings of the National Academy of Sciences. 104, 19210–19213.

Humle, T., Maisels, F., Oates, J.F., Plumptre, A., Williamson, E.A., 2016. Pan troglodytes. The IUCN

Red List of Threatened Species.

Hunt, K.D., McGrew, W.C., 2002. Chimpanzees in the dry habitats of Assirik, Senegal and Semliki Wildlife Reserve, Uganda. In: Boesch, C., Hohmann, G., Marchant, L.F. (Eds.), Behavioural Diversity in Chimpanzees and Bonobos. Cambridge University Press, Cambridge, pp. 35–51.

Huxley, T.H., 1863. Evidence as to Man's Place in Nature. D. Appleton, New York.

Isbell, L.A., Young, T.P., 1996. The evolution of bipedalism in hominids and reduced group size in chimpanzees: alternative responses to decreasing resource availability. Journal of Human Evolution. 30, 389–397.

Itani, J., 1979. Distribution and adaptation of chimpanzees in an arid area (Ugalla area, Western Tanzania. In: Hamburg, D.A., McCown, E.R. (Eds.), The Great Apes. Benjamin/Cummings, Menlo Park, pp. 52–72.

Kalan, A.K., Kulik, L., Arandjelovic, M., Boesch, C., Haas, F., Dieguez, P., Barratt, C.D., Abwe, E.E., Agbor, A., Angedakin, S., Aubert, F., Ayimisin, E.A., Bailey, E., Bessone, M., Brazzola, G., Buh, V.E., Chancellor, R., Cohen, H., Coupland, C., Curran, B., Danquah, E., Deschner, T., Dowd, D., Eno-Nku, M., Michael Fay, J., Goedmakers, A., Granjon, A.C., Head, J., Hedwig, D., Hermans, V., Jeffery, K.J., Jones, S., Junker, J., Kadam, P., Kambi, M., Kienast, I., Kujirakwinja, D., Langergraber, K.E., Lapuente, J., Larson, B., Lee, K.C., Leinert, V., Llana, M., Marrocoli, S., Meier, A.C., Morgan, B., Morgan, D., Neil, E., Nicholl, S., Normand, E., Ormsby, L.J., Pacheco, L., Piel, A., Preece, J., Robbins, M.M., Rundus, A., Sanz, C., Sommer, V., Stewart, F., Tagg, N., Tennie, C., Vergnes, V., Welsh, A., Wessling, E.G., Willie, J., Wittig, R.M., Yuh, Y.G., Zuberbühler, K., Kühl, H.S., 2020. Environmental variability supports chimpanzee behavioural diversity. Nature Communications. 11, 1–10.

Kano, T., 1971. The chimpanzee of Filabanga, western Tanzania. Primates. 12, 229–246.

Knott, C.D., 2005. Energetic responses to food availability in the great apes : implications for hominin evolution, Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates. In: Brockman, D.K., van Schaik, C.P. (Eds), Cambridge University Press, Cambridge. pp 351–378.

Kortlandt, A., 1983. Marginal Habitats of Chimpanzees. Journal of Human Evolution. 12, 231–278.

Leakey, L.S.B., 1970. The relationship of african apes, man, and old world monkeys. Proceedings of the National Academy of Sciences. 67, 746–748.

Lefebvre, L., Reader, S.M., Sol, D., 2004. Brains, innovations and evolution in birds and primates. Brain, Behavior and Evolution. 63, 223–246.

Lehmann, J., Boesch, C., 2004. To fission or to fusion: Effect of community size on wild chimpanzee (*Pan troglodytes versus*) social organisation. Behavioral Ecology and Sociobiology. 56, 207–216.

Lindshield, S., Hernandez-Aguilar, R.A., Korstjens, A.H., Marchant, L.F., Narat, V., Ndiaye, P.I., Ogawa, H., Piel, A.K., Pruetz, J.D., Stewart, F.A., van Leeuwen, K.L., Wessling, E.G., Yoshikawa, M., 2021. Chimpanzees (*Pan troglodytes*) in savanna landscapes. Evolutionary Anthropology.

Marchant, L.F., Wessling, E.G., Lindshield, S.M., 2020. Introduction to the special issue on savanna chimpanzees. International Journal of Primatology. 41, 767–774.

Martínez, L., Pauline, Í., Harmonie, B., Simone, K., Tobias, P., 2021. Intercommunity interactions and killings in central chimpanzees (*Pan troglodytes troglodytes*) from Loango National Park, Gabon. Primates. 1–14

McGrew, W.C., 1979. Evolutionary implications of sex differences in chimpanzee predation and tool use. In: Hamburg, D., McCown, E. (Eds.), The Great Apes. Benjamin/Cummings, Menlo Park, pp. 440–463.

McGrew, W.C., 2010. Chimpanzee technology. Science. 328, 579–580.

McGrew, W.C., Baldwin, P.J., Tutin, C.E.G., 1981. Chimpanzees in a dry, hot and open habitat: Mt. Assirik, Senegal, West Africa. Journal of Human Evolution. 10, 227–244.

Mitani, J.C., 2013. Chimpanzee models of human behavioral evolution. In: Sponheimer, M., Lee-Thorp, J.A., Reed, K.E., Ungar, P.S. (Eds.), Early Hominin Paleoecology. University Press of Colorado, Boulder, pp. 397–435.

Moore, J., 1992. Savanna Chimpanzees. In: Nishida, T., McGrew, W.C., Marler, P., Pickford, M., de Waal, F.B.M. (Eds.), Topics in Primatology, Vol. I: Human Origins. Tokyo Press University, Tokyo, pp. 99–118.

Moore, J., 1996. Savanna chimpanzees , referential models and the last common ancestor. In: McGrew, W.C., Marchant, L.F., Nishida, T. (Eds.), Great Ape Societies. Cambridge University Press, Cambridge, pp. 275–292.

Moore, J.F., Mulindahabi, F., Gatorano, G., Niyigaba, P., Ndikubwimana, I., Cipolletta, C., Masozera, M.K., 2018. Shifting through the forest: home range, movement patterns, and diet of the eastern chimpanzee (*Pan troglodytes schweinfurthii*) in Nyungwe National Park, Rwanda. American Journal of Primatology. 80, 1–13.

Muller, M.N., Wrangham, R.W., Pilbeam, D., 2017. Chimpanzees and Human evolution. Harvard University Press, Cambridge.

Nakamura, M., Corp, N., Fujimoto, M., Fujita, S., Hanamura, S., Hayaki, H., Hosaka, K., Huffman, M.A., Inaba, A., Inoue, E., Itoh, N., Kutsukake, N., Kiyono-Fuse, M., Kooriyama, T., Marchant, L.F., Matsumoto-Oda, A., Matsusaka, T., McGrew, W.C., Mitani, J.C., Nishie, H., Norikoshi, K., Sakamaki, T., Shimada, M., Turner, L.A., Wakibara, J. V., Zamma, K., 2013. Ranging behavior of Mahale chimpanzees: A 16 year study. Primates. 54, 171–182.

Nishida, T., 1968. The social group of wild chimpanzees in the Mahale Mountains. Primates. 9, 167–224.

Nishida, T., 1983. Alpha status and agonistic alliance in wild chimpanzees (*Pan troglodytes schweinfurthii*). Primates. 24, 318–336.

Nishida, T., 2012. Chimpanzees of the lakeshore: Natural history and culture at Mahale. Cambridge University Press, Cambridge.

Piel, A.K., Strampelli, P., Greathead, E., Hernandez-aguilar, R.A., Moore, J., Stewart, F.A., 2017. The diet of open-habitat chimpanzees (*Pan troglodytes schweinfurthii*) at Issa, Ugalla, western Tanzania. Journal of Human Evolution. 112, 57–69.

Plavcan, J.M., 2013. Reconstructing social behavior from fossil evidence. In: Begun, D.R. (Ed.), A Companion to Paleoanthropology. Blackwell Publishing, Chichester, pp. 226–243.

Potts, K.B., Baken, E., Levang, A., Watts, D.P., 2016. Ecological factors influencing habitat use by chimpanzees at Ngogo, Kibale National Park, Uganda. American Journal of Primatology. 78, 432–440.

Potts, R., 1998. Environmental hypotheses of hominin evolution. American Journal of Physical Anthropology. 107, 93–136.

Poulson, J.R., Clark, C.J., Smith, T.B., 2001. Seasonal variation in the feeding ecology of the grey-cheeked mangabey (*Lophocebus albigena*) in Cameroon. American Journal of Primatology. 54, 91–105.

Pruetz, J.D., 2006. Feeding ecology of savanna chimpanzees. In: Hohmann, G., Robbins, M.M., Boesch, C. (Eds.), Feeding Ecology in Apes and Other Primates. Cambridge University Press, Cambridge, pp. 161–182.

Pruetz, J.D., 2007. Evidence of cave use by savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal: Implications for thermoregulatory behavior. Primates. 48, 316–319.

Pruetz, J.D., 2021. Water conservation: Human water balance exceeds that of other apes. Current Biology. 31, 389–391.

Pruetz, J.D., Bertolani, P., 2009. Chimpanzee (*Pan troglodytes verus*) behavioral responses to stresses associated with living in a savannah-mosaic environment: Implications for hominin adaptations to open habitats. PaleoAnthropology. 252–262.

Pruetz, J.D., Bertolani, P., Ontl, K.B., Lindshield, S., Shelley, M., Wessling, E.G., 2015. New evidence on the tool-assisted hunting exhibited by chimpanzees (*Pan troglodytes verus*) in a savannah habitat at Fongoli, Senegal. Royal Society Open Science. 2, 1–11.

Reed, K.E., 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. Journal of Human Evolution. 32, 289–322.

Reynolds, V., 2006. The Chimpanzees of Budongo. Oxford University Press, Oxford.

Robinson, J.R., Rowan, J., Campisano, C.J., Wynn, J.G., Reed, K.E., 2017. Late Pliocene environmental change during the transition from Australopithecus to Homo. Nature Ecology & Evolution. 1, 1–7.

Russak, S., 2013. Ecological role of dry-habitat chimpanzees (*Pan troglodytes schweinfurthii*). Arizona

State University.

Sayers, K., Lovejoy, C.O., 2008. The chimpanzee has no clothes. Current Anthropology. 49, 87–114.

Schoeninger, M.J., Reeser, H., Hallin, K., 2003. Paleoenvironment of *Australopithecus anamensis* at Allia Bay, East Turkana , Kenya : evidence from mammalian herbivore enamel stable isotopes. Journal of Anthropological Archaeology. 22, 200–207.

Sept, J.M., 1992. Was there no place like home? A new perspective on early hominid archaeological sites from the mapping of chimpanzee nests. Current Anthropology. 33, 187–207.

Sponheimer, M., Loudon, J.E., Codron, D., Howells, M.E., Pruetz, J.D., Codron, J., de Ruiter, D.J., Lee-Thorp, J.A., 2006. Do “savanna” chimpanzees consume C4 resources? Journal of Human Evolution. 51, 128–133.

Stanford, C.B., 1995. The influence of chimpanzee predation on group size and anti-predator behaviour in red colobus monkeys. Animal Behaviour. 49, 577–587.

Stephens, D.W., Krebs, J.R., 1986. Foraging Theory. Princeton University Press, Princeton.

Stevenson, P.R., Quinones, M.J., Ahumada, J.A., 1994. Ecological strategies of woolly monkeys (*Lagothrix lagotricha*) at Tinigua National Park, Colombia. Journal of Primatology. 32, 123–40.

Suzuki, A., 1969. An ecological study of chimpanzees in a savanna woodland. Primates. 10, 103–148.

Thompson, M.E., Jones, J.H., Pusey, A.E., Brewer-Marsden, S., Goodall, J., Marsden, D., Matsuzawa, T., Nishida, T., Reynolds, V., Sugiyama, Y., Wrangham, R.W., Drive, N.F., 2007. Aging and fertility patterns in wild chimpanzees provide insights into the evolution of menopause. Current Biology. 17, 2150–2156.

Thompson, N.E., Demes, B., O’Neill, M.C., Holowka, N.B., Larson, S.G., 2015. Surprising trunk rotational capabilities in chimpanzees and implications for bipedal walking proficiency in early hominins. Nature Communications. 6, 1–7.

Ungar, P.S., Sponheimer, M., 2011. The diets of early hominins. Science. 334, 190–193.

van Leeuwen, K.L., Hill, R.A., Korstjens, A.H., 2020. Classifying chimpanzee (*Pan troglodytes*) landscapes across large-scale environmental gradients in Africa. International Journal of

Primatology. 41, 800–821.

van Schaik, C.P., Brockman, D.K., 2005. Seasonality in primate ecology, reproduction, and life history: an overview. In: Brockman, D K, van Schaik, C P (Eds.), Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates. Cambridge University Press, Cambridge, pp. 3–20.

van Schaik, C.P., Terborgh, J.W., Wright, S.J., 1993. The phenology of tropical forests : adaptive significance and consequences for primary consumers. Annual Review of Ecology and Systematics. 24, 353–377.

Wallis, J., 1997. A survey of reproductive parameters in the free-ranging chimpanzees of Gombe National Park. Journal of reproduction and fertility. 109, 297–307.

Watts, D.P., Mitani, J.C., 2001. Boundary patrols and intergroup encounters in wild chimpanzees. Behaviour. 138, 299–327.

White, T.D., Asfaw, B., Beyene, Y., Haile-Selassie, Y., Lovejoy, C.O., Suwa, G., WoldeGabriel, G., 2009. *Ardipithecus ramidus* and the paleobiology of early hominids. Science. 326, 64–86.

Wilson, M.L., 2021. Insights into human evolution from 60 years of research on chimpanzees at Gombe. Evolutionary Human Sciences. 3, 1–26.

Wittig, R.M., 2018. 40 years of research at the Taï Chimpanzee Project. Pan Africa News. 25, 16–18.

Wrangham, R.W., Jones, J.H., Laden, G., Pilbeam, D., Conklin-Brittain, N., 1999. The raw and the stolen: cooking and the ecology of human origins. Current Anthropology. 40, 567–594.

Wrangham, R., Peterson, D., 1996. Demonic Males: Apes and the Origins of Human Violence. Houghton Mifflin Company, Boston.

Wrangham, R.W., 1977. Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In: Clutton-Brock, T. (Ed.), Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes. Academic Press, London. pp. 503–538.

Wrangham, R.W., 2000. Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In: Kappeler, P. (Ed.), Primate Males: Causes and Consequences of Variation in Group Composition. Cambridge University Press, Cambridge, pp. 248–258.

Chapter 2: General methods, study location and environmental data

In this chapter I first introduce the study site and subjects as well as the general methods. For the present study, I collected behavioral data on Issa chimpanzees as well as environmental data within the study site. Abiotic factors, such as rainfall and temperature, greatly affect the availability of resources (food and water), which in turn largely determine chimpanzee ecology (Wrangham, 1986). I thus briefly describe the environmental variables recorded during the study period: rainfall, temperature, food and water availability. Because later in this thesis I will compare Issa chimpanzee behavior to the behavior of chimpanzees at other sites, I contextualize here some general environmental characteristic at Issa by comparing them to other chimpanzee sites. Furthermore, an understanding of how environmental factors change over time is a necessary step towards understanding the fluctuations and determinants of chimpanzees social, ranging, and feeding behavior. Accordingly, I test whether each environmental variable (climate and resource availability) is characterized by a seasonal pattern (seasonality refers to recurrent climate fluctuations that tend to have a period of one year) and describe their temporal fluctuations.

1. Geography

The Issa study area lies 100km East of Lake Tanganyika, within the Greater Mahale Ecosystem, in western Tanzania (Figure 2.1). The first long term study was conducted in 2001 by Hernandez-Aguilar (Hernandez-Aguilar, 2006) but there has been a continuous research presence only since 2008 (Piel *et al.*, 2018). Initially classified as “general land” (Stewart, 2011), in 2018 it became subsumed within the Tongwe West Forest Reserve.

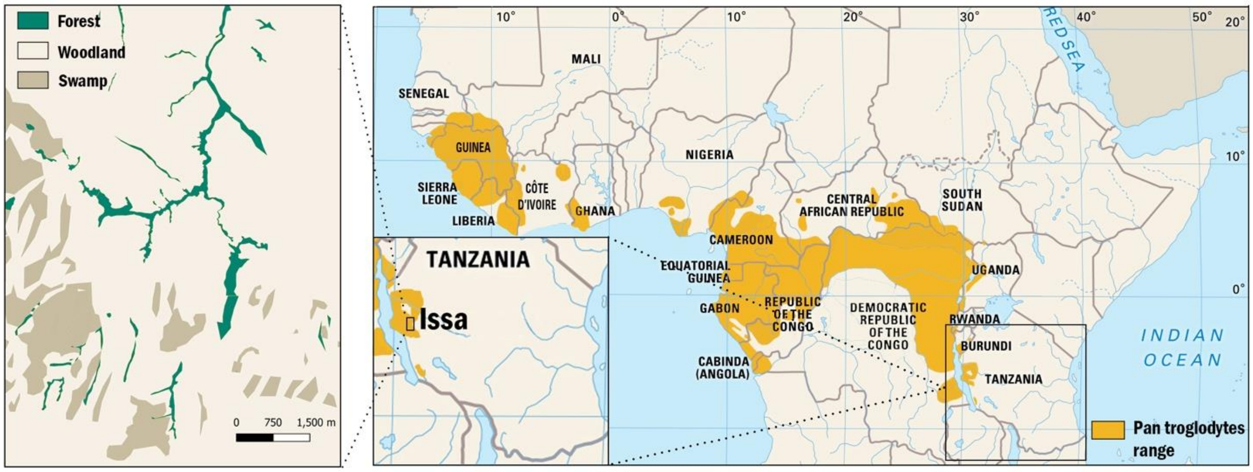


Figure 2.1 Map of chimpanzee (*Pan troglodytes*) distribution (in yellow), with Tanzania and Issa study area (black boxes). Source: Humle *et al.*, (2016)

2. Vegetation and habitat

The region consists of broad valleys separated by steep mountains and flat hilltop plateaus and is characterized by a mosaic vegetation dominated by "miombo" woodland. Miombo is the local name to refer to species of *Brachystegia* and *Julbernardia*. In the present study, I classified vegetation into three categories (see Figure 2.2): swamp (8% of the area), woodland (85%), and forest (7%) (vegetation class layer produced by Caspian Johnson, unpublished) and grouped swamp and woodland into the open habitat structure while forest was defined as closed habitat.

Figure 2.2 Issa three habitat categories (swamp, woodland, and forest). © R. Delahunty

3. Subjects

When data collection began, the Issa community was comprised of twenty-six chimpanzees: eight adult females, seven adult males, three subadult males, five juveniles and three infants (Figure 2.3). Given that the community was fully habituated only in the beginning of 2018 (when individuals could be followed from morning to nightly nest and from within 15 meters), I do not have birth records nor exact age information of community members; I thus estimated ages and classified them in the following categories: adult: > 11 years, adolescent: 8–11 years, juvenile: 4–7 years, infant: < 4 years (following Sugiyama, 1999). One subadult female joined the community in October 2018, one adult female disappeared in January 2019, and one adult female gave birth in March 2019. The Issa community home range was estimated at 36km^2 at the time of study (see Chapter 4). Although direct measures of predator density have not been made, Issa site hosts four potential predators for chimpanzees: lions (*Panthera leo),* leopards (*Panthera pardus),* hyenas (*Crocuta crocuta*) and wild dogs (*Lycaon pictus)* (Piel *et al.*, 2018).

Figure 2.3 Pictures of the 20 adults and subadults in the Issa community during the study period

4. Behavioral follows

I collected behavioral data between March 2018 and May 2019 but used only data from June 2018 to May 2019 for Chapter 3 and 4; and from May 2018 to May 2019 for Chapter 5, because I could not obtain enough data points at the beginning of the study period. When their sleeping location was known, we reached chimpanzees at their nests before sunrise and followed them during the day (Figure 2.4) until their next nesting site when possible. Alternatively, we listened and located chimpanzees from vocalizations and checked recently used feeding sites. Typically, the field team consisted of two people who were focusing on collecting different data and communicated through radio. We performed instantaneous scan samples at 15-min intervals (Altmann, 1974) and recorded party size, presence of swollen females, activity, feeding occurrences and habitat type. Each day we also attempted a focal follow (Altmann, 1974) of an adult or subadult chimpanzee. We randomly chose a focal individual from the first party encountered and followed him/her for as long as possible, ideally until s/he built a night nest. Focal chimpanzee locations were recorded at 5-min intervals using the GNSS receiver of an Android tablet (CUBOT MTK6753A). If the focal individual was lost during a follow, every attempt was made to regain contact, but if this was not possible within 30 minutes, we selected a new individual to follow.

Figure 2.4 CG following a chimpanzee party and collecting behavioral data at Issa. © C. Lile

Three types of behavioral data were collected: data on diet (Chapter 3), ranging (Chapter 4) and party size (Chapter 5).

5. Climate

Issa is described as one of the driest, most open, and seasonal habitats inhabited by chimpanzees (Russak, 2013). An electronic rain gauge (Onset Corp., HOBO, model RH3) was deployed to monitor climate and recorded every 2 mm of rainfall during the study period. A temperature logger (Onset Corp.) was also deployed to record temperature at 30-min intervals. Both were located inside the core chimpanzee home range, in the woodland habitat.

Issa site is historically described as a savanna site (Hernandez-Aguilar, 2006), but the term “savanna” includes a variety of ecosystems ranging from open grasslands to closed woodlands (Moore, 1992). As suggested by van Leeuwen *et al.*, (2020), I contextualize Issa’s environmental characteristics by comparing them to other chimpanzee sites. I extracted from van Leeuwen et al. (2020) the values reported at 42 chimpanzees sites for the following variables: total annual rainfall, number of dry months, average temperature and percentage of forest cover; and compared them to Issa values.

The percentage of forest cover at Issa (7%) is much lower than what is found elsewhere on average (mean: 57.46 ± 37.47%, range: 2–100%) but similar to other sites classified as savannas (Figure 2.5). When compared to the average at other sites (mean: 4.36 ± 1.48, range: 1–7), the number of consecutive dry months at Issa (6) is extreme with only two sites among the 42 described in Figure 2.5 having larger values (*i.e.*, seven months for Bafing and Mount Assirik). Annual precipitation at Issa (1220mm) is low compared to the average (mean: 1706.56 ± 516.05mm, range: 750–3244mm) but some sites classified as savanna are characterized by even lower values. Annual mean temperature (23°C) is close to the global mean at all sites (mean: 24.04°C ± 2.79, range: 16.3–29°C); this is the lowest mean temperature among all sites classified as savanna, and there are many sites classified as forest that are on average hotter than Issa.

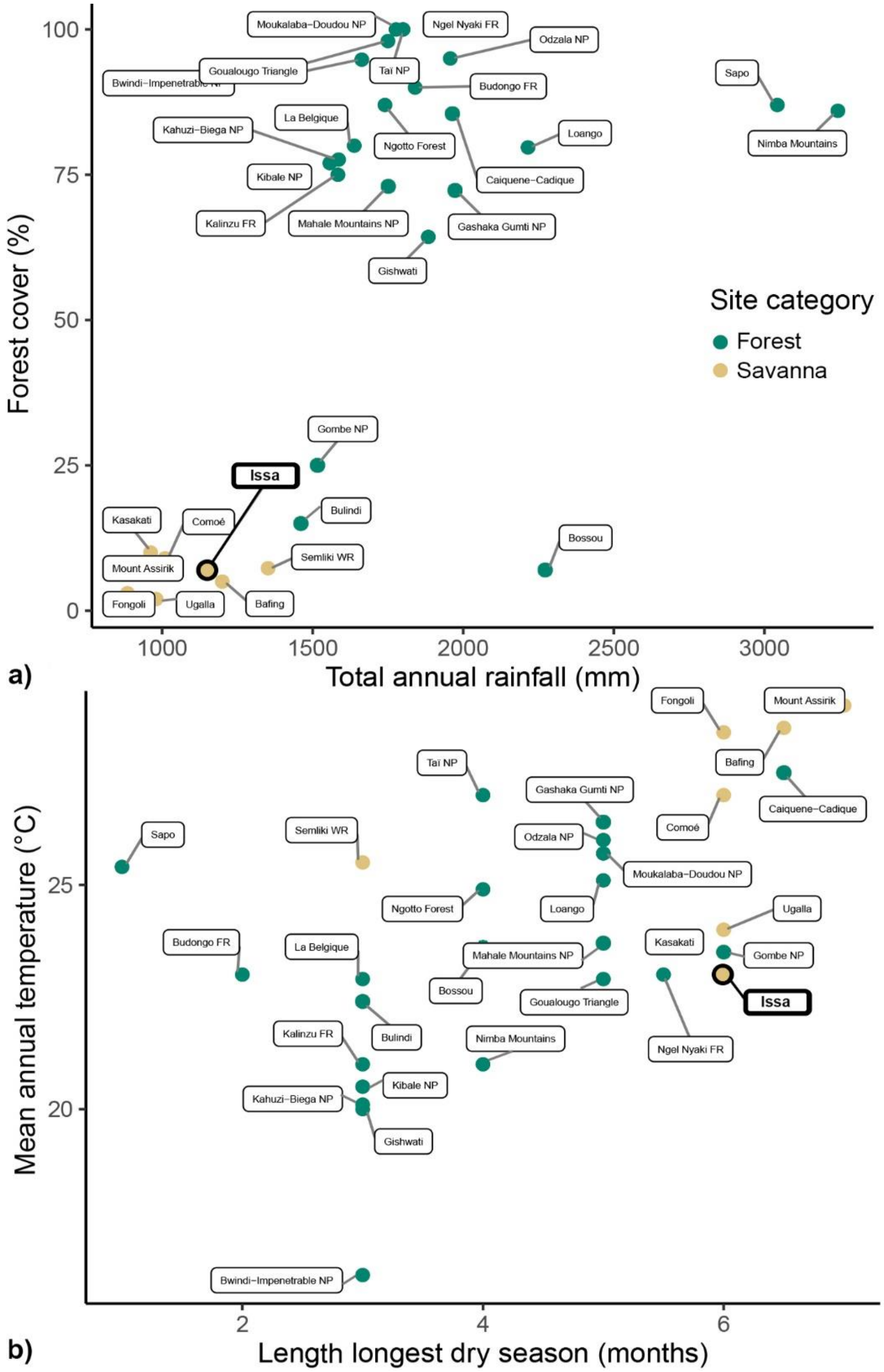


Figure 2.5 Relationships of (a) total annual rainfall vs. forest cover and (b) length of the longest dry season vs. mean annual temperature at selected chimpanzee sites, labeled with the site classifications (savanna: yellow; forest: green) used by researchers (modified after van Leuween *et al.* 2020)

6. Seasonality in climatic variables

To test whether climatic variables (*i.e.*, daily rainfall, daily minimum temperature, daily mean temperature, and daily maximum temperature) varied seasonally, I fitted generalized linear models in R v. 3.4.0 (R Core Team, 2017) using the function 'glm' with a Gaussian error function and tested for the effect of the seasonal term on each response variable. The seasonal term was represented by both sine and cosine of Julian date (divided by 365.25 and then multiplied by 2π; Stolwijk *et al.*, 1999; Wessling *et al.*, 2018) to which the data corresponded. It assumes regular periodicity in a single annual cycle. I checked for the assumptions of independent and homogeneous residuals by visually inspecting q–q plots and the residuals plotted against fitted values and found no violations. I performed Chi–square tests using the R function 'anova' to determine the significance of each model compared to corresponding null models.

Table 2.1 Effect of season on environmental variables measured at Issa

Variable ~1 + sine (Julian date) + cosine (Julian date)	F*	*p*
Temperature (daily maximum, ˚C)[a]	57.77	< 0.001
Temperature (daily minimum, ˚C)[b]	125.91	< 0.001
Temperature (daily mean, ˚C)[c]	33.66	< 0.001
Daily rainfall (mm)[d]	3935.6	< 0.001

* Degrees of freedom: 2, 395.
[a]Mean ± SD: 28.91 ± 2.71, range: 19.6–35.6 [b]Mean ± SD: 15.25 ± 1.85, range: 10.08–18.79
[c]Mean ± SD: 20.14 ± 1.48, range: 17.26–24.54 [d]Mean ± SD: 3.21 ± 8.49, range: 0–67.21

All climatic variables were seasonal during the study period (Table 2.1). Rains occurred mainly in November–April (Figure 2.6). Although temperature at Issa did not show extreme variations, it was characterized by a seasonal pattern with the hottest temperatures in September–October, and coolest ones in July–August (Figure 2.6). These seasonal fluctuations in weather, and particularly in rainfall, are likely to have an impact on the phenology of the plant community, and thus on the abundance, nature, and distribution of potential chimpanzee food items.

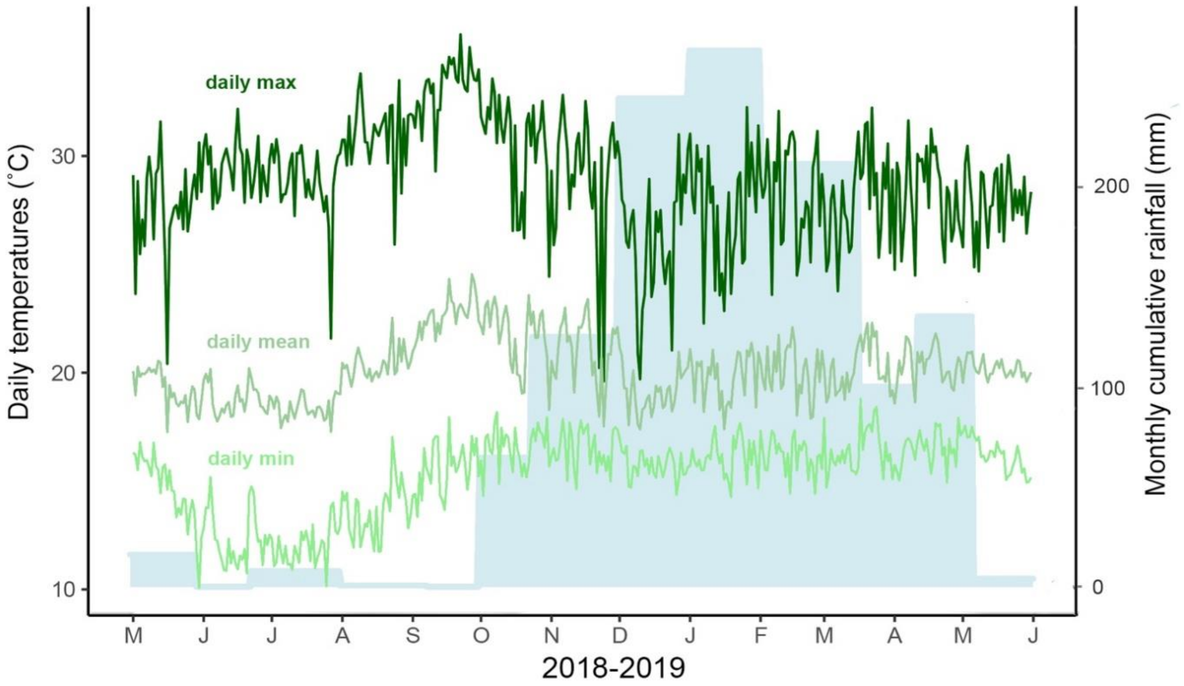


Figure 2.6 Variation over the study period (May 2018–May 2019) of daily temperatures (in °C, daily maximum: dark green; daily mean: green; daily minimum: light green) and monthly cumulative rainfall (in mm; blue).

7. Resource availability

To assess the food resources available for Issa chimpanzees and their fluctuations during the study periods, I calculated a food availability index (FAIe).

Basal area

To calculate FAIe, I first needed to obtain plant species basal areas. From 2013 to 2019, 306 plots (20 × 20 m) were botanically sampled across the study site. Plots were randomly sampled inside each vegetation category, *i.e.*, forest, woodland, and swamp. All stems with a diameter at breast height (DBH) > 10 cm were identified and measured. I calculated a mean DBH for each species. I obtained species density estimates in each vegetation category ($D_{sforest}$, $D_{swoodland}$, D_{sswamp}) and extrapolated species density (D_s) in the whole area based on cover percentage of each vegetation category *i.e.*, 7% forest cover, 85%

woodland, 8% swamp: $D_s = 0.07 \times D_{sforest} + 0.85 \times D_{swoodland} + 0.08 \times D_{sswamp}$. I followed Basabose (2002) and calculated global basal area (BA_s) for each species s using the formula:

$$BA_s = (\frac{1}{2} \times DBH_s)^2 \times \pi \times D_s.$$

Important plant food items

I calculated a FAIe based on the most important plant food items in the Issa chimpanzee diet. A plant food item was defined as a distinct plant part (*e.g.*, fruit, flower, leaf) and species. I chose to focus only on the most frequently consumed items because some rarely consumed species are overly represented in the Issa landscape (*e.g.*, *Brachystegia microphylla*: basal area: 2.8 m^2 per ha *versus* 0.26 % of total diet), which would have overestimated food availability during months when these species produce feeding items. To measure dietary composition, we performed a group scan every 15 minutes, and recorded if a feeding occurrence was happening at the time the scan (see Chapter 3). I calculated annual intake of each food item as the number of 15-minutes scans in which said item was consumed as a proportion of all feeding scans (Emery Thompson and Wrangham, 2008). I then defined important food items as those that cumulatively made up 75% of the total annual diet (Wrangham *et al.*, 1996; Newton-fisher, 1999). Thirteen plant food items were selected trough this criterion (see Chapter 3).

Phenology

On a monthly basis, phenological changes in plant food items were monitored inside chimpanzee territory using phenological trails. The percent abundance (0 = 0%, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, 4 = 76–100%) of each item in the crown of individual trees was estimated. The trails were different from phenological transects as they were non-systematic and targeted only key species based on previous estimation of Issa chimpanzee diet from indirect observations (Piel *et al.*, 2017). The full habituation of the community and the results of the present study allowed us to acknowledge that three items from the important items list (the three less frequently eaten, *i.e.*, fruits of *Englerophytum magalismontanum, Syzygium guineense and Landolphia owariensis*) were not present in the phenological trails (see Chapter

3). I thus could not record their monthly phenological changes and include them in the FAIe calculation. However, these items represented only 4% of the total diet during the study period. FAIe was therefore calculated using only the top 10 plant food items, on 288 individual trees (with a minimum of five individuals per species, see Table 2.2).

Nutritional value

I followed Knott's (2005) suggestion and included item nutritional value to calculate monthly FAIe. For this purpose, I collected samples of the top 10 feeding items for later macro-nutrient analyses. For each sample I collected as many units (one unit is defined as *e.g.*, one single fruit, one single leaf, *etc.*) as possible of the same maturity stage or as close as possible, and processed the items in the same way as a chimpanzee would (*e.g.*, remove seeds, peel, *etc.*) following Rothman *et al.* (2011). Whenever it was possible, for each item, I got samples from a least two different trees. Also, when chimpanzees were observed consuming the same item over multiple days, I collected samples from at least two different days whenever possible. For *Ficus* species especially, as individual trees are asynchronous and fig fruits can be found almost all year round, I tried to collect a different sample each month the chimpanzees were seen eating figs. I dried all samples using an electric dehydrator and weighed them at the field station before sending them to the nutritional laboratory of the Institute for Zoo and Wildlife Research in Berlin, for energy content analysis.

We assessed gross energy by burning the samples in pure oxygen atmosphere in a bomb calorimeter (C5003 bomb calorimeter; IKA–Werke GmbH & Co. KG, Staufen, Germany). We measured the heat produced in kJ/g of dry matter (see Table 2.2). Although I acknowledge that spatiotemporal variations in composition can occur for the same food item from different trees and/or at different times, for the ease of the study, I pooled all samples from the same food item to obtain the mean energy content for each item.

Food availability index

I calculated food availability index (FAIe) based on the 10 most eaten items by using the following formula:

$$FAIe_m = \sum_{1}^{10} P_{ism} \times BA_{si} \times M_i \times E_i$$

where P_{im} denotes the mean abundance of item *i* on species *s* in month *m*, BA_{si} represents the basal area per hectare in Issa area for the species s to which the item i belongs, M_i represents the average dry mass for item *i* and E_i the average energy per gram of dry mass for item *i*.

Table 2.2 Top 10 feeding items used for FAIe calculation and their corresponding proportion in total diet (*i.e.*, proportion of feeding scans) during the study period, average energy (kJ per gram of dry mass), average dry mass (g), number of units used for macronutrient (MN) analyses, corresponding species basal area (cm^2 per ha) and number of individuals trees in phenological trails.

Species	**Part**	**% of scans**	**Energy (kJ/g)**	**Mass (g)**	***n* unit MN analyses**	**Basal area (cm2/ha)**	***n* ind. trees in phen. trails**
Ficus spp.*	fruit	31	17.90	0.62	1007	256.10	11
Garcinia huillensis	fruit	9	17.28	0.16	160	523.88	33
Pterocarpus tinctorius	flower	6	20.89	0.06	500	2603.35	29
Saba comorensis	fruit	4	18.81	11.18	16	3.46	5
Diplorhynchus condylocarpon	fruit	4	20.39	0.83	32	646.82	33
Brachystegia spiciformis	leaf	4	21.41	0.05	600	3725.38	29
Parinari curatellifolia	fruit	3	18.19	2.41	35	4450.48	116
Flacourtia indica	fruit	2	18.90	0.88	125	36.20	8
Julbernardia unijugata	fruit	2	20.92	0.09	200	2359.58	15
Cordia africana	fruit	2	18.09	3.15	26	210.85	9

* I grouped all *Ficus* trees into a single category, as we were unable to determine species for all *Ficus* trees.

Water availability

Water availability is also likely to have an impact on Issa chimpanzee temporal fluctuations in behavior. I assessed water availability fluctuations inside Issa range during the study period, by calculating a water availability index (WAI) following Wessling *et al.* (2018). Each month, I monitored the depths (at the deepest point) of eight water sources in the Issa community home range and calculated WAI using the following equation:

$$WAI_m = \sum_{1}^{8} \frac{Depth_{im}}{Depth_{\max[i]}}$$

where $Depth_{im}$ denotes the depth of source i for month m and $Depth_{max[i]}$ the maximum observed depth for source i. WAI ranges from zero (no ground water available) to one (maximum water available).

8. Seasonality in resources availability

Using the same methodology as per the test of climatic variables seasonality, I tested whether overall FAIe, the availability of each of the top 10 important plant food items, and WAI varied seasonally, by fitting generalized linear models using the R function ‘glm’ with a Poisson error function and tested for the effect of a seasonal term on each response variable.

Table 2.3 Effect of season on food (FAIe) and water (WAI) availability indexes, and on the availability of the top 10 important plant food items

Variable ~1 + sine (Julian date) + cosine (Julian date)	χ^{2}*	P
FAIe	323.170	< **0.001**
WAI	382.412	< **0.001**
Brachystegia spiciformis leaf	223.720	< **0.001**
Cordia africana fruit	23.141	< **0.001**
Diplorhynchus condylocarpon fruit	7.541	< **0.001**
Ficus spp. fruit	0.916	0.328
Flacourtia indica fruit	18.919	< **0.001**
Garcinia huillensis fruit	258.200	< **0.001**
Julbernardia unijugata fruit	11.571	< **0.001**
Parinari curatellifolia fruit	26.963	< **0.001**
Pterocarpus tinctorius flower	18.919	< **0.001**
Saba comorensis fruit	30.454	< **0.001**

* Degrees of freedom: 2, 13.

FAIe and WAI at Issa were highly seasonal (Table 2.3, FAIe: mean ± SD: 336832.87 ± 456750.57, range: 2493.66–1538781.00; WAI: mean ± SD: 0.66 ± 0.23, range: 0.20–0.94). I observed a peak in food availability in November 2018 and there were two periods of very low food availability: May–July 2018 and January–March 2019 (Figure 2.7). WAI was the highest in February 2019 and the lowest at the end of the dry season in October 2018 (Figure 2.7). Although water was very low and/or stagnant in some areas of the home range in October, it remained available and flowing at the majority of the points where I measured WAI.

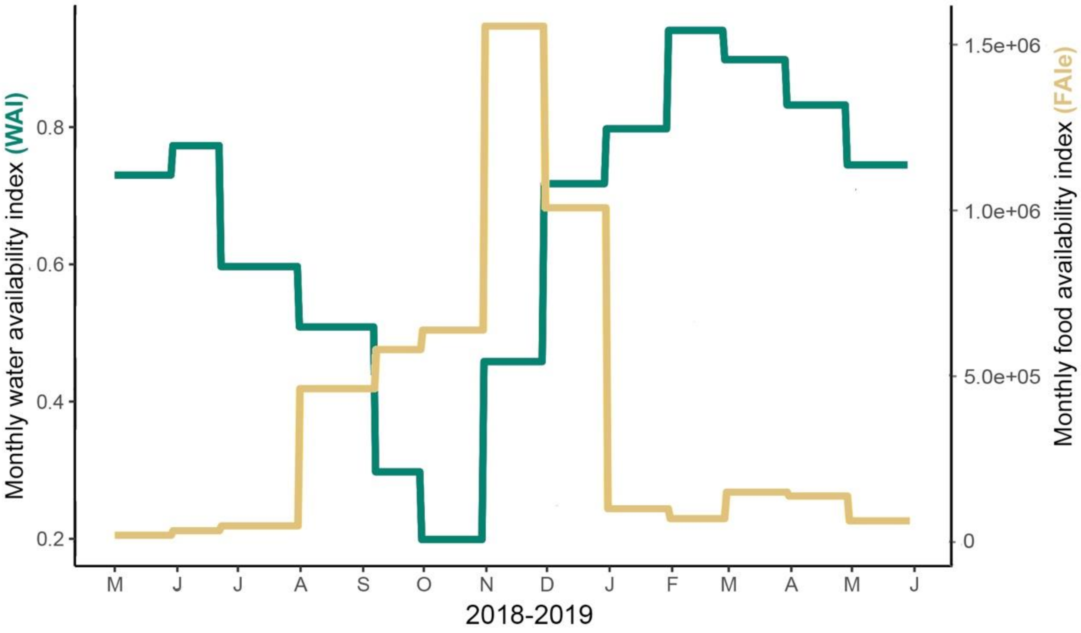


Figure 2.7 Variation over the study period (May 2018–May 2019) of monthly top 10 food availability index (FAIe, in yellow) and water availability index (WAI, in green) at Issa site.

The availability of all important plant food items was seasonal expect the for the *Ficus* spp. fruit (Table 2.3), that was available almost every month of the study period (Figure 2.8)

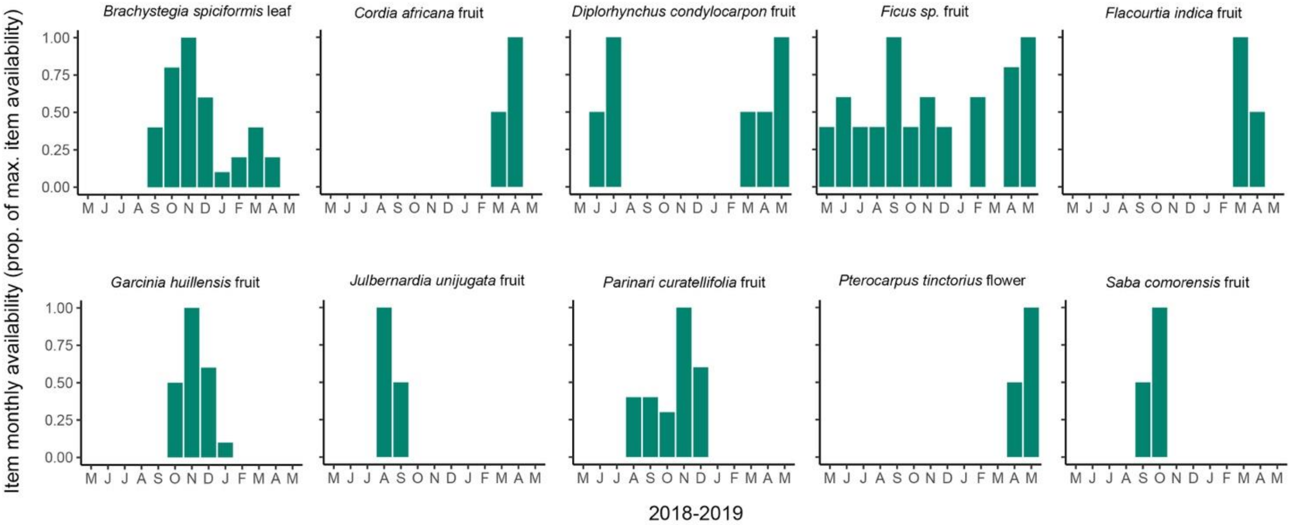


Figure 2.8 Seasonality in the availability of the ten most important plant feeding items for Issa chimpanzees over the study period, May 2018–May 2019 (illustrated is the proportion of each item availability compared to the maximum availability for the given item during the study period).

In summary, comparisons between chimpanzee savanna-woodland sites suggested that Issa is as dry and open but not as hot as other savanna-woodland sites. I confirmed that rainfall at Issa was highly seasonal as well as food and water availability during the study period. All the important plant food items showed seasonal patterns in their availability, except for *Ficus* spp. fruit. Such an arid and open landscape characterized by seasonality in resource availability is likely to influence Issa chimpanzee diet, ranging and grouping patterns, all of which I will explore in the following chapters.

9. References

Altmann, J., 1974. Observational study of behavior: sampling methods. Behaviour. 49, 227–267.

Basabose, A.K., 2002. Diet composition of chimpanzees inhabiting the montane forest of Kahuzi, Democratic Republic of Congo. American Journal of Primatology. 58, 1–21.

Emery Thompson, M., Wrangham, R.W., 2008. Diet and reproductive function in wild female chimpanzees (*Pan troglodytes schweinfurthii*) at Kibale National Park, Uganda. American Journal of Physical Anthropology. 135, 171–181.

Hernandez-Aguilar, R.A., 2006. Ecology and nesting patterns of chimpanzees (*Pan troglodytes*) in Issa, Ugalla, western Tanzania. University of Southern California, CA.

Humle, T., Maisels, F., Oates, J.F., Plumptre, A., Williamson, E.A., 2016. *Pan troglodytes*. The IUCN Red List of Threatened Species.

Knott, C.D., 2005. Energetic responses to food availability in the great apes : implications for hominin evolution, Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates. In: Brockman, D.K., van Schaik, C.P. (Eds), Cambridge University Press, Cambridge. pp. 351–378

Moore, J., 1992. Savanna Chimpanzees. In: Nishida, T., McGrew, W.C., Marler, P., Pickford, M., de Waal, F.B.M. (Eds.), Topics in Primatology, Vol. I: Human Origins. Tokyo Press University, Tokyo, pp. 99–118.

Newton-Fisher, N.E., 1999. The diet of chimpanzees in the Budongo Forest Reserve, Uganda. African Journal of Ecology. 37, 344–354.

Piel, A.K., Bonnin, N., Amaya, S.R., Wondra, E., Stewart, F.A., 2018. Chimpanzees and their mammalian sympatriates in the Issa Valley, Tanzania. African Journal of Ecology. 57, 31–40.

Piel, A.K., Strampelli, P., Greathead, E., Hernandez-Aguilar, R.A., Moore, J., Stewart, F.A., 2017. The diet of open-habitat chimpanzees (*Pan troglodytes schweinfurthii*) at Issa, Ugalla, western Tanzania. Journal of Human Evolution. 112, 57–69.

Rothman, J.M., Chapman, C.A., Soest, P.J. Van, 2011. Methods in primate nutritional ecology: A user's guide. International Journal of Primatology. 33, 542–566.

Russak, S., 2013. Ecological role of dry-habitat chimpanzees (*Pan troglodytes schweinfurthii*). Arizona State University.

Stewart, F.A., 2011. The evolution of shelter: ecology and ethology of chimpanzee nest building. University of Cambridge.

Stolwijk, A.M., Straatman, H., Zielhuis, G.A., 1999. Studying seasonality by using sine and cosine functions in regression analysis. Journal of Epidemiology and Community Health. 53, 235–238.

Sugiyama, Y., 1999. Socioecological factors of male chimpanzee migration at Bossou, Guinea. Primates. 40, 61–68.

van Leeuwen, K.L., Hill, R.A., Korstjens, A.H., 2020. Classifying chimpanzee (*Pan troglodytes*) landscapes across large-scale environmental gradients in Africa. International Journal of Primatology. 41, 800–821.

Wessling, E.G., Kühl, H.S., Mundry, R., Deschner, T., Pruetz, J.D., 2018. The costs of living at the edge : Seasonal stress in wild savanna-dwelling chimpanzees. Journal of Human Evolution. 121, 1–11.

Wrangham, R.W., 1986. Ecology and social relationship in two species of chimpanzee. In: Rubenstein, D.I., Wrangham, R.W. (Eds.), Ecological Aspects of Social Evolution. Princeton University Press, Priceton, pp. 352–378.

Wrangham, R.W., Chapman, C.A., Clark-Arcadi, A.P., Isabirye-Basuta, G., 1996. Social ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups. In: McGrew, W.C., Marchant, L.F., Nishida, T. (Eds.), Great Ape Societies. Cambridge University Press, Cambridge, pp. 45–57.

Chapter 3: Issa chimpanzee dietary responses to seasonal fluctuations in resources abundance.

To be submitted in summer 2022 to the International Journal of Primatology for publication

1. Introduction

To survive and reproduce, primates must consume sufficient nutrients (Hemingway and Bynum, 2005). Understanding primate feeding behavior is central to almost every aspect of their biology (Altmann and Altmann, 1970; Hamilton, 1985; Hemingway and Bynum, 2005), and can be used, for instance, to predict species social behavior (Wrangham, 1980; Isbell, 1991), inter-species interactions (Schreier *et al.*, 2009), or ranging (Ganas and Robbins, 2005).

Because they mostly rely on vegetative foods, primates face temporal variations in food abundance and quality (Clutton-Brock and Harvey, 1977; Terborgh and Janson, 1986), and food shortages often have negative repercussions on energy balance, fecundity, growth and survival (Altmann, 1998; Wallis, 2002; Hemingway and Bynum, 2005; Knott, 2005). To limit these impacts and maintain sufficient nutrient and energy intake during lean periods, primates exhibit a large range of adaptations including adjusting their group size (Aureli *et al.*, 2008) and/or ranging behavior via modifications of their daily path length or home range size (Hemingway and Bynum, 2005). More commonly, individuals may respond to resource availability fluctuations by being flexible in their diet. Indeed, most species do not depend on the same food type year-round but instead adapt and consume resources as they become available (Hill, 1997). For instance, because of its richness in non-structural carbohydrates and relatively low fiber content, fruit is an important food for many primates (Richard, 1985), but individuals often face temporal shortages in its availability (van Schaik *et al.*, 1993) and respond to these periods by switching to alternative food sources (Hemingway and Bynum, 2005). Primates may switch among food categories (*e.g.*, fruit to leaves or insects, leaves to bark, *etc.*) or within the same category (*e.g.*, from one fruit species to another). For instance, Japanese macaques (*Macaca fuscata*) predominantly consume fruits, seeds, insects, or leaves depending on the time of the year (Hill, 1997).

To better understand primate feeding ecology, researchers not only document the plant species and parts consumed by primates, but also evaluate the type and amount of macronutrients these items provide (Ortmann and Bradley, 2006). Various laboratory methods have been developed to determine the macronutrient composition of food, and involve drying, burning, and chemical procedures (Ortmann and

Bradley, 2006). Non-structural carbohydrates, proteins, fats and fibers are the main macronutrients assessed to define food quality and are usually expressed as a percentage of the dry matter (Rothman *et al.*, 2011). Carbohydrates are a major source of energy (Milton, 1993). In the primate nutrition literature, they are often divided into non-structural and structural carbohydrates (fibers) (Ortmann and Bradley, 2006). The first category is usually easily digested and provides readily available energy, whereas structural carbohydrates are indigestible by the animal's own enzymes but may be fermented with the aid of symbiotic gut micro-organisms in some species (Lambert, 1998). Protein is an important nutrient as many of its constituent amino acids are required for maintenance of body tissues. Protein intake is crucial for primates (and other animals) because they either fail to synthesize some essential amino acids or do not produce them in the quantities required to meet their needs (Ortmann and Bradley, 2006). Fats are also important energy sources for primates; they have the highest energy density among dietary components but most plant foods do not have appreciable quantities of fat, aside from some fatty fruits, seeds, or nuts (National Research Council, 2003). Finally, fibers are typically a marker of a poor nutritive quality as fiber content is expected to be inversely related to the digestibility of a food item (van Soest, 1994).

Food quality not only depends on the macronutrient composition but also on the facility in extraction (*e.g.*, if it requires a tool to be extracted, hard *versus* soft shell, *etc.*) and digestion (Conklin-Brittain *et al.*, 1998; Wrangham *et al.*, 1998). Nuts for instance are highly nutritious for chimpanzees but require the use of tools (*e.g.*, hammer and anvil) to be opened before consumption (Boesch and Boesch, 1983). Leaves, pith, and bark are usually rich in proteins but dense in fibers, particularly cellulose and hemicellulose, which are difficult to digest and are thus usually considered low-quality foods (Milton, 1993). Fruits, on the contrary, because they are rich in non-structural carbohydrates are considered high quality and preferred food items for many primate species (Lambert, 1998). Preferred foods are those selected more frequently than expected relative to their availability, whereas fallback foods (FBFs) are those consumed when preferred food items are not available and are generally assumed to be of lower nutritional quality and/or harder to digest and extract (Lambert, 2007; Marshall and Wrangham, 2007;

Marshall *et al.*, 2009). FBFs have been suggested to have both ecological and evolutionary implications, because their exploitation is often critical to the survival of individuals during lean periods (Marshall *et al.*, 2009). These definitions do not reflect a given food's importance, *i.e.*, its contribution to the total diet (Marshall and Wrangham, 2007; Marshall *et al.*, 2009). Important items are those that are eaten the most frequently. Researchers use different methods to determine them: for instance Wrangham *et al.* (1996) and Newton-Fisher (1999) used the items that cumulatively contributed to >75% of feeding time, while Potts *et al.* (2011) or Wakefield (2010) respectively considered the top 10 or 20 species in the diet. Preferred foods are not necessarily important foods; they may be important (high contribution in the diet) during periods when they are available, but also of low importance when they become scarce. Similarly, FBF can be important foods especially during periods of preferred food scarcity.

Chimpanzees (*Pan troglodytes*) are omnivorous primates that primarily consume fruit (Harrison and Marshall, 2011). Particularly, fleshy fruits are frequently consumed because of their high nutritional value and particularly their richness in non-structural carbohydrates (Wrangham *et al.*, 1993; Basabose, 2002; Reynolds, 2006; Chancellor *et al.*, 2012). Despite being predominantly frugivorous, chimpanzees also demonstrate dietary flexibility (Harrison and Marshall, 2011). Across their distribution, chimpanzees consume leaves, flowers, meat, bark, stems, terrestrial herbaceous vegetation (THV), insects, mushrooms, *etc.* (Conklin-Brittain *et al.*, 1998; Wrangham *et al.*, 1998; Basabose, 2002; Knott, 2005; Pruetz, 2006; Matthews *et al.*, 2019). When preferred food is scarce, chimpanzees typically rely on FBFs (Marshall *et al.*, 2009), but the type of FBF they use varies across communities. For instance, insects have been suggested to be a FBF at Kahuzi-Biega, DRC (Yamagiwa and Basabose, 2009), while they are preferred at other sites (*e.g.*, Gashaka, Nigeria: Sommer *et al.*, 2017; Fongoli, Senegal: Bogart and Pruetz, 2011). Similarly, figs have been classified as FBF at Kanyawara, Uganda, but as a preferred food at Nyungwe, Rwanda (Matthews *et al.*, 2019) and Kahuzi-Biega (Yamagiwa and Basabose, 2009). In Bossou, Guinea, oil palm fruit, nut and pith were the most important FBFs (Yamakoshi, 1998), while Malenky and Wrangham (1991) suggested that THV was the major FBF in Kibale, Uganda.

Overall, chimpanzee dietary responses during food scarcity periods, vary greatly across communities. This likely depends on inter-site variation in food nutritional composition, on the availability and diversity of food items, or on the length and severity of food scarcity (Tutin *et al.*, 1997; Chapman *et al.*, 1999). Accordingly, chimpanzee feeding ecology needs to be examined in relationship to local ecological characteristics and the availability and nutrient content of chimpanzee foods. Chimpanzees range across a wide variety of habitats from closed rainforests to open and dry savanna-woodland habitats (van Leeuwen *et al.*, 2020; Lindshield *et al.*, 2021). Detailed knowledge of chimpanzee diet and behavior are primarily derived from forest habitats (*e.g.*, Boesch and Boesch-Achermann, 2000; Newton-Fisher *et al.*, 2000; Watts *et al.*, 2012b). In savanna-woodlands, which are highly seasonal habitats (Bourliere and Hadley, 1983), with fewer food species (in number and species diversity) compared to forested environments (Isbell and Young, 1996; Wessling *et al.*, 2020), specific behavioral feeding adaptations to cope with decreased food availability are likely to emerge (Lindshield *et al.*, 2021). For instance, studies at savanna-woodland sites revealed that chimpanzees in these habitats seem to have a narrower diet than chimpanzees elsewhere (see Table 3.1)

Table 3.1 Comparison of the diet breadth (in number of different plant species) in different chimpanzee communities

Community	Habitat	Diet breadth	Method	Source
Assirik	Savanna	43	Fecal analysis + feeding remains + obs.	McGrew *et al.*, 1988
Bossou	Forest	200	Behavioral follow	Sugiyama and Koman, 1992
Budongo (Sonso)	Forest	53	Behavioral follow	Newton-fisher, 1999
Fongoli	Savanna	47	Fecal analysis + feeding remains + obs.	(Pruetz, 2006)
Gombe	Forest	103	Behavioral follow	(Stumpf, 2011)
Issa	Savanna	78	Behavioral follow + fecal analysis	this study + (Piel *et al.*, 2017)
Kahuzi-Biega	Forest	114	Fecal analysis + feeding remains + obs.	(Basabose, 2002)
Kibale (Kanyawara)	Forest	112	Fecal analysis + feeding remains + obs.	(Wrangham *et al.*, 1991)
Kibale (Ngogo)	Forest	102	Behavioral follow	(Watts *et al.*, 2012b)
Mahale (M-Group)	Forest	198	Behavioral follow	Matsumoto-Oda and Kasagula, 2000
Nyungwe	Forest	93	Behavioral follow	Matthews *et al.*, 2019
Taï (North)	Forest	223	Behavioral follow	Boesch *et al.*, 2006

Obs: Opportunistic observations

Additionally, chimpanzees in the savanna-woodland landscape of Fongoli have been observed to utilize invertebrate prey more than chimpanzees elsewhere (Pruetz, 2006; Bogart and Pruetz, 2011), and chimpanzees at Issa may use tools to extract and consume underground storage organs (USOs) (Hernandez-Aguilar *et al.*, 2007). However, to date, the information we have on chimpanzee feeding ecology in savanna-woodland habitats relies primarily on indirect data from macroscopic fecal analysis, feeding remains or opportunistic observations (McGrew *et al.*, 1988; Pruetz, 2006; Hernandez-Aguilar *et al.*, 2007; Piel *et al.*, 2017). These methods underestimate overall dietary diversity, often missing highly digestible items and having bias in the identifications of leaf, pith, and bark species (Phillips and McGrew, 2014). To understand the feeding strategies of chimpanzees in savanna-woodlands, where food availability is scarcer and varies seasonally more than in other, more tropical areas, we need data from direct observations.

The present study is the first to use direct observations to document the feeding ecology of the Issa chimpanzee community, in western Tanzania. The objectives of this study were to:

(1) determine Issa chimpanzees general diet, including their important, preferred, and FBFs;
(2) assess whether macronutrient composition may influence food selection;
(3) assess how temporal changes in food abundance influence chimpanzee’s diet.

I hypothesized that if Issa chimpanzees are limited by their dry, open and seasonal habitat in terms of plant food species diversity and abundance, their plant-based diet would be narrower than at more forested sites and they would rely highly on FBFs such as leaves, THV, insects, and possibly USOs during periods of preferred food scarcity. Furthermore, given the marked seasonal fluctuations in climate and food availability (see Chapter 2), I hypothesize that Issa chimpanzee diet will vary greatly throughout the year. I predicted that Issa chimpanzees will generally prefer fruits, as it is the case at other sites, because fruits have high nutritional value compared to non-preferred foods and particularly higher content of non-structural carbohydrates and lower content of fiber. Inversely, I hypothesized that FBFs would have high content of fiber and low content of non-structural carbohydrates.

2. Material and methods

2.1. Data collection

Behavioral observations

Data collection spanned 12 months, from June 2018 to May 2019. We looked for and followed chimpanzee parties on average 20 days/month. When their sleeping location was known, we reached chimpanzees at their nests before sunrise and followed them during the day until their next nesting site when possible. Alternatively, we listened and located chimpanzees from vocalizations and checked feeding sites. We performed instantaneous scan samples at 15-min intervals (Altmann, 1974). During scans, we recorded all adult and subadult individuals in the party who were feeding and identified the food item(s). A food item was defined as a distinct plant part and species or a distinct type of non-plant food (*e.g.*, termite). Specimens of *Ficus* spp. were identified only to genus level because we could not distinguish species in the field. Food items fell into eight categories: fruit, leaf, flower, THV, bark, invertebrate, vertebrate, and fungus. We recorded a feeding occurrence for a given food item if one or more individuals were observed feeding on it at the time of the scan (Gilby *et al.*, 2014). Over the study period, we gathered 1913 feeding occurrences during our 15-minutes instantaneous scans.

Plant density and phenology

To assess plant species density and basal area, 306 botanic plots (20 × 20 m) were samples across the study site (see Chapter 2). On a monthly basis, phenology of plant species for Issa chimpanzees was monitored by recording phenological changes in 288 individual trees inside the home range using phenological trails previously established (see Chapter 2).

Food item sampling

I collected food items that Issa chimpanzees were observed feeding on (see detailed methods in Chapter 2). I dried all samples using an electric dehydrator and weighed them at the field station before sending them to the nutritional laboratory of the Institute for Zoo and Wildlife Research in Berlin for energy and macronutrient analysis. Although I acknowledge that spatiotemporal variations in macronutrient composition can occur for the same food item (Chapman *et al.*, 2003), for the ease of the study, I pooled all samples from the same food item to obtain the mean nutrient and energy content for each item. The lab technician at IZW, Heidrun Barleben and I conducted the analyses.

Energy and macronutrient content

Samples were ground to a fine powder (see Appendix Figure 3.A.7) to conduct the analyses following Ortmann and Bradley (2006). We determined dry matter content by drying a portion of each sample at 105°C over-night and all macronutrient contents are expressed as % of dry matter. We assessed gross energy by burning the samples in a pure oxygen atmosphere in a bomb calorimeter (C5003 bomb calorimeter; IKA–Werke GmbH & Co. KG, Staufen, Germany) and measured the heat produced in kJ/g of dry matter (see Appendix Figure 3.A.8).

For estimation of protein content, we determined nitrogen content via Dumas' combustion technique (Buckee, 1994) at high temperature (950°C) in pure oxygen, using a Rapid N III analyzer (Elementar Analyser Systeme GmbH, Hanau, Germany) (see Appendix Figure 3.A.9). This technique results in volatilization of all nitrogen in the sample as gas (N_2), which is then detected and measured as mass (g) or percentage (%). Assuming that all N_2 from the sample comes from proteins and amino acids, we used the factor 6.25 to convert nitrogen content into crude protein: crude protein (% dry matter) = 6.25 × N (% dry matter).

For estimation of fat content, we extracted total fats by repeatedly washing the samples with petroleum ether in a fully automatic Soxhlet system (Soxtherm; Gerhardt Laboratory Systems, Königswinter, Germany) (see Appendix Figure 3.A.100): fat content (% dry matter) = extracted fat weight (g) ×100/dry sample weight (g).

We estimated non-structural carbohydrates, namely sucrose, D-glucose, D-fructose, and starch with commercialized enzymatic tests (R–Biopharm, Darmstadt, Germany; UV method) (see Appendix Figure 3.A.11).

For assessment of crude fiber, we sequentially digested petroleum ether-washed, fat-free samples in sulfuric acid and sodium hydroxide (to eliminate non-structural components) (see Appendix Figure

3.A.12); samples were then left to dry, and subsequently burnt at 550°C for 2 h in a muffle oven, which removed all the organic matter and left the inorganic residue (ashes). We then calculated crude fiber content as:

Crude fiber (% dry matter) = [digested sample weight (g) – ashes weight (g)]×100/dry sample weight (g).

Finally, we estimated the mineral content of the samples as the weight of the inorganic residue (ashes).

2.2. Data analysis

<u>Diet composition</u>

I determined monthly diet using the number of 15-minutes scans where each food item was eaten divided by the number of scans with feeding occurrences per month (Emery Thompson and Wrangham, 2008). I calculated the annual diet using the mean percentage of feeding occurence for each item category across the 12 study months.

<u>Diet quality</u>

I looked at the macronutrient composition of the different food categories (*i.e.*, fruit, leaf, flower, insect, THV, and fungus) eaten by Issa chimpanzees (except vertebrate meat, given the impossibility of obtaining a sample) to assess their nutritional quality. I estimated the proportion of non-structural carbohydrates (as the sum of glucose, fructose, sucrose and starch), proteins and fats because of their nutritional relevance, and also crude fiber content, as high level of fibers are frequently negatively correlated with diet quality because they are difficult to digest (Lambert, 1998).

<u>Important foods</u>

Following Wrangham *et al.* (1996) and Newton-Fisher (1999), I defined important foods as those cumulatively contributing to >75% of the feeding occurrences, and created monthly and annual lists. I also looked at the nutritional composition of important foods using the methods described above.

Diet seasonality

To test whether consumption of different important items and food categories varied seasonally, I fitted generalized linear models on R v. 3.4.0 (R Core Team, 2017) separately for each variable using the function 'glm' with a Poisson error function. I tested for the effect of a seasonal pattern on each response variable by including a seasonal term represented by both sine and cosine of Julian date (divided by 365.25 and then multiplied by 2π) (Stolwijk *et al.*, 1999; Wessling *et al.*, 2018b) to which the data correspond. This seasonal term assumes regular periodicity in a single annual cycle. I checked for the assumptions of independent and homogeneous residuals by visually inspecting Q–Q plots and the residuals plotted against fitted values and found no violations. I performed *Chi*–square tests using the R function 'anova' to determine the significance of each model compared to corresponding null models. I used a Bonferroni-corrected significance value ($p<0.0017$).

Food availability

I calculated the monthly availability of each food item (FA_{im}) using the following formula:

$$FA_{im} = P_{ism} \times BA_{si}$$

where P_{ism} denotes the mean abundance of item i on species s in month m, and BA_{si} represents the basal area per hectare in Issa area for the species s to which the item i belongs.

Preferred foods

To determine the preferred food items in Issa chimpanzee's diet, I used a rank preference index (RPI, Johnson, 1980). For a given item in a given month, I calculated the difference between its ranked consumption (1 to n; 1 being most consummed) and ranked availability (1 to n; 1 being most available), and then averaged this difference for the number of months that the item was available (Johnson, 1980). If RPI was below zero, the item was considered preferred.

Nutritional value of preferred foods compared to non preferred foods

I performed Wilcoxon rank tests or *t*–tests (depending on the normality and heteroscedasticity of the variables) to compare preferred (N=10) and non preferred (N=11) foods for energy, protein, fat, starch, glucose, fructose, sucrose, mineral, and crude fiber contents. I set significance value at $p<0.006$ (Bonferroni-corrected).

Preferred food availability index

Monthly, I calculated a preferred food availability index *(PFAIe*) based on the sum of the monthly availability of all preferred foods in Issa chimpanzee's diet. I followed Knott's (2005) suggestion and included item nutritional value in the calculation of the monthly preferred food availability index. I used the following formula:

$$PFAIe_m = \sum PFA_{im} \times M_i \times E_i$$

where PFA_{im} denotes the availability of preferred item *i* in month *m*, M_i represents the average dry mass for preferred item *i* and E_i represents the average energy per gram of dry mass for preferred item *i*.

Fallback foods

Food categories were considered FBFs when their consumption increased when preferred foods were less available (Altmann, 1998; Marshall *et al.*, 2009). To determine whether certain food categories constituted FBFs, I fitted generalized linear models separately for each category using the function 'glm' of the R program with a quasipoisson error function and setting the significance level alpha at Bonferroni-corrected value of 0.01. I tested for the effect of preferred food availability on the response variable: consumption of each potential FBF. I also included the seasonal term previously described to account for the regular periodicity in a single annual cycle of the item consumption. I checked for the assumptions of independent and homogeneous residuals by visually inspecting Q–Q plots and the residuals plotted against fitted values and found no violations. I performed *Chi*–square tests using the R function 'anova' to determine the significance of each model compared to corresponding null models.

3. Results

3.1. Diet description, important food items and nutritional composition

We observed chimpanzees consume 70 plant food items (Table 3.2) from 48 plant species, as well as termites (*Macrotermes subhyalinus*), ants (*Camponotus* sp.), yellow baboon (*Papio cynocephalus*), red-tailed monkey (*Cercopithecus ascanius*), bushbuck (*Tragelphus scriptus*), and various unidentified species of fungi. During the study period we did not record any occurrence of USO extraction and/or consumption by Issa chimpanzees. Overall, chimpanzees consumed fruits (72% of 1913 total observations), followed by leaves (11%), flowers (7%), insects (4%), THV (2%), vertebrates (1%), fungi (<1%), and occasional other items such as bark and fecal matter (coprophagy). Fruits in general had the greatest proportion of non-structural carbohydrates, but were low in proteins compared to the other categories (Figure 3.1).

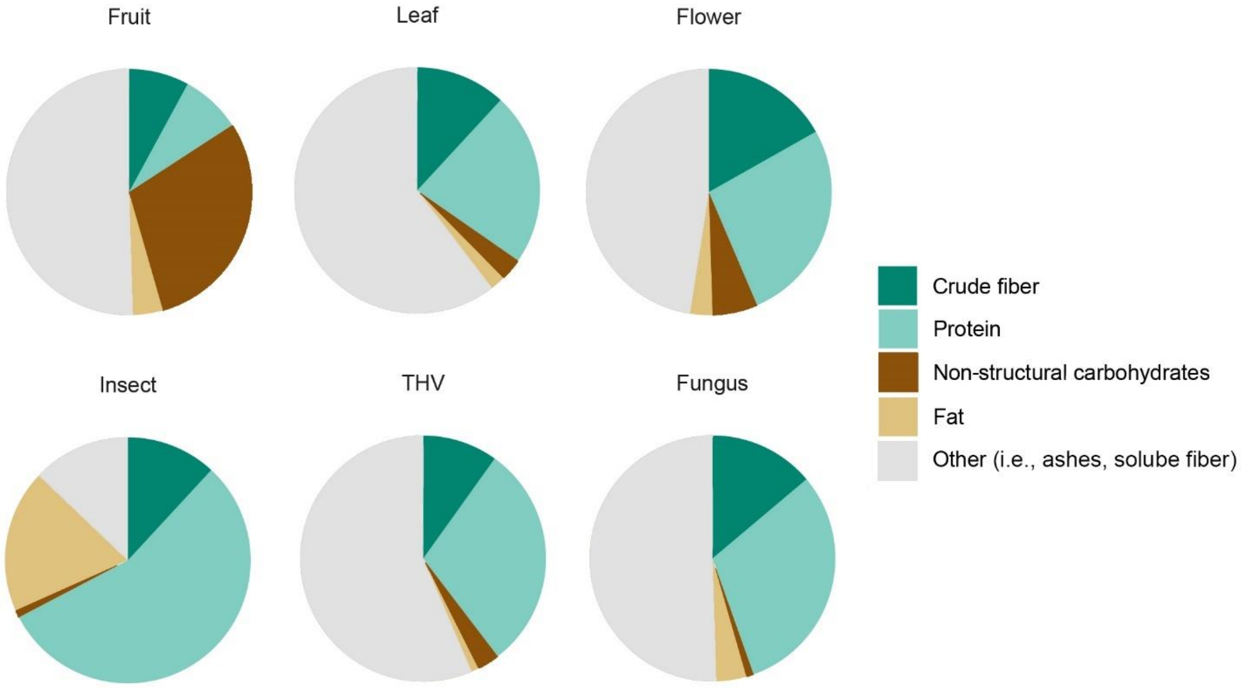


Figure 3.1 Proportion in dry matter of macronutrients (fat, non-structural carbohydrates, and protein) and crude fiber in the different food categories eaten by Issa chimpanzees, from June 2018 to May 2019.

Table 3.2 Comprehensive Issa chimpanzees diet list during the study period (June 2018–May 2019).

Category	Scientific name	Common name	Plant parts
Vertebrate	*Cercopithecus ascanius*	Red-tailed monkey	
	Papio cynocephalus	Yellow baboon	
	Tragelphus scriptus	Bushbuck	
Fungus	Unknown		
Insect	*Camponotus* sp.	Ant	
	Macrotermes subhyalinus	Termite	
Plant	*Afrocanthium burttii*		fruit
	Afromomum mala		fruit, stem
	Anisophyllea boehmii		fruit
	Annona senegalensis		fruit
	Bauhinia thonningii		fruit
	Berchemia discolor		fruit
	Borassus aethiopum		fruit
	Brachystegia bussei		bark
	Brachystegia longifolia		fruit
	Brachystegia spiciformis		bark, flower, fruit, leaf
	Brachystegia utilis		bark, fruit, leaf
	Canthium hispidum		fruit
	Combretum molle		flower, fruit
	Cordia africana		fruit
	Diplorhynchus condylocarpon		fruit, leaf
	Englerophytum magalismontanum		fruit
	Ficus spp.		bark, fruit, leaf
	Flacourtia indica		flower, fruit
	Garcinia huillensis		fruit, leaf
	Grewia sp.		fruit
	Hexalobus monopetalus		fruit
	Julbernardia globiflora		flower, leaf
	Julbernardia unijugata		fruit
	Keetia ferruginea		fruit
	Keetia gueinzii		fruit
	Landolphia owariensis		fruit
	Maesopsis eminii		fruit
	Monopetalanthus richardsiae		fruit, leaf
	Newtonia buchananii		fruit, leaf
	Parinari curatellifolia		fruit
	Pteridium aquilinum		leaf, stem
	Pterocarpus angolensis		fruit, leaf
	Pterocarpus tinctorius		flower, fruit, leaf
	Saba comorensis		fruit
	Sclerocarya birrea		fruit
	Strychnos innocua		fruit
	Strychnos sp.		fruit
	Syzygium guineense		fruit
	Thespesia sp.		bark, fruit
	Uapaca kirkiana		fruit
	Uapaca nitida		fruit
	Uvaria angolensis		fruit
	Vitex doniani		fruit, leaf
	Vitex mombassae		fruit
	Ximenia americana		fruit
	Ximenia caffra		fruit, leaf
	Zanha africana		fruit

The annual top fourteen food items accounted for 75% of the total diet (Table 3.3). *Ficus* spp. fruit was the most important item in the diet (31% of total diet and 42% of all fruits scans) followed by *Garcinia huillensis* fruit. Among non-fruit items, flowers of *Pterocarpus tinctorius*, young leaves of *Brachystegia spiciformis*, and *Macrotermes subhyalinus* termites were also important in the total annual diet.

Table 3.3 The fourteen most important feeding items in Issa chimpanzees' annual diet (items that cumulatively make 75% of diet) during the study period (June 2018–May 2019) ordered by importance in the diet (in %); among which are indicated preferred feeding items (mean RPI <0) and items used for the calculation of preferred food availability index (PFAIe).

Species	Part	Imp. in diet (%)	RPI	Preferred	Used for PFAIe
Ficus spp.	fruit	31	– 1.8	Yes	Yes
Garcinia huillensis	fruit	9	– 0.2	Yes	Yes
Pterocarpus tinctorius	flower	6	– 0.3	Yes	Yes
Macrotermes subhyalinus	termite	4		Yes[a]	
Saba comorensis	fruit	4	– 1.8	Yes	Yes
Diplorhynchus condylocarpon	fruit	4	0.3		
Brachystegia spiciformis	leaf	4	2.5		
Parinari curatellifolia	fruit	3	1.3		
Flacourtia indica	fruit	2	– 0.7	Yes	Yes
Julbernardia unijugata	fruit	2	0.5		
Cordia africana	fruit	2	– 0.3	Yes	Yes
Englerophytum magalismontanum	fruit	2		Yes[b]	
Landolphia owariensis	fruit	2		Yes[b]	
Syzygium guineense	fruit	2		Yes[b]	
Cumulative	–	75	–	–	–

a This item is only hypothesized to be preferred because chimpanzees systematically fed on it when it was available, but termite availability could not be calculated and compared to plant item availability.

b These items are only hypothesized to be preferred because we systematically observed chimpanzees frequently feeding on them when they were available, but no phenological data could be collected for these items (they appeared to be important *a posteriori* and were thus initially not included into phenological trails).

The main contributor to the diet, *Ficus* spp. fruit, presented a high content of crude fiber, but a relatively low of non-structural carbohydrates, compared to other fruits (Figure 3.2). The food items with the highest protein contents were the flowers of *P. tinctorius*, leaves of *B. spiciformis*, and termites, while fat content was highest also in termites, and in the fruits of *E. magalismontanum* (Figure 3.2).

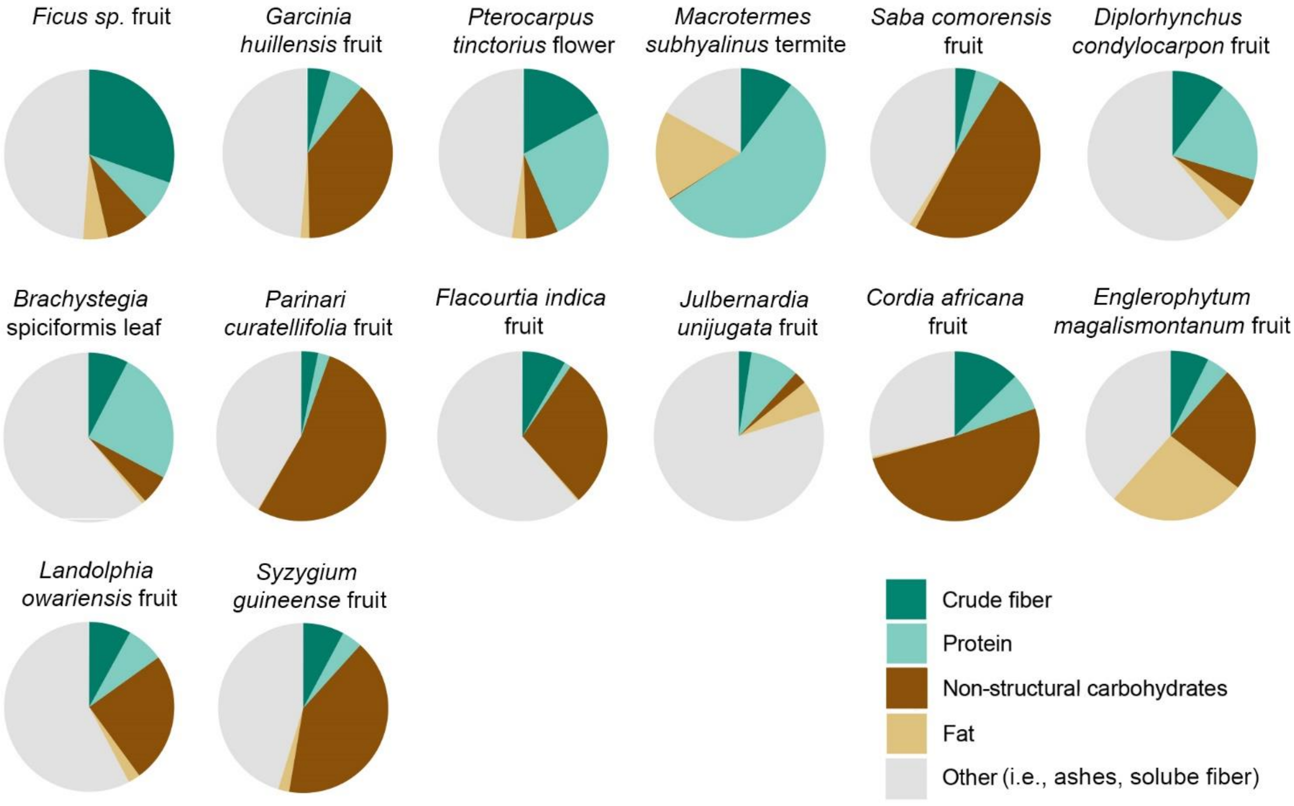


Figure 3.2 Proportion in dry matter of macronutrients (*i.e.*, fat, non-structural carbohydrates, and protein) and crude fiber in the important food items in Issa chimpanzees' diet.

3.2. Seasonal variation in dietary composition

The diet of Issa chimpanzees changed monthly (see Appendix Table 3.A.6 for detailed monthly diets). Leaves, flowers, insects, vertebrates and fungi were consumed seasonally, whereas fruit and THV consumption did not show any statistically significant seasonal pattern (Table 3.4, Figure 3.3).

Chimpanzees consumed the most leaves from August–October (mainly *B. speciformis* and *P.tinctorius* young leaves). There was minimal (and in some cases, none at all) flower consumption throughout the year except in March and April, where it represented more than 30% of the monthly diet (mainly *P. tinctorius* flowers). Insects were most frequently eaten during the termite fishing season from October–December. Issa chimpanzees were observed hunting vertebrates in September–December. Fungi were incorporated in the diet only in December, January and March. Regarding the consumption of important food items, I observed seasonality in the consumption of all important items tested, except *Ficus* spp. fruits and leaves (Table 3.4).

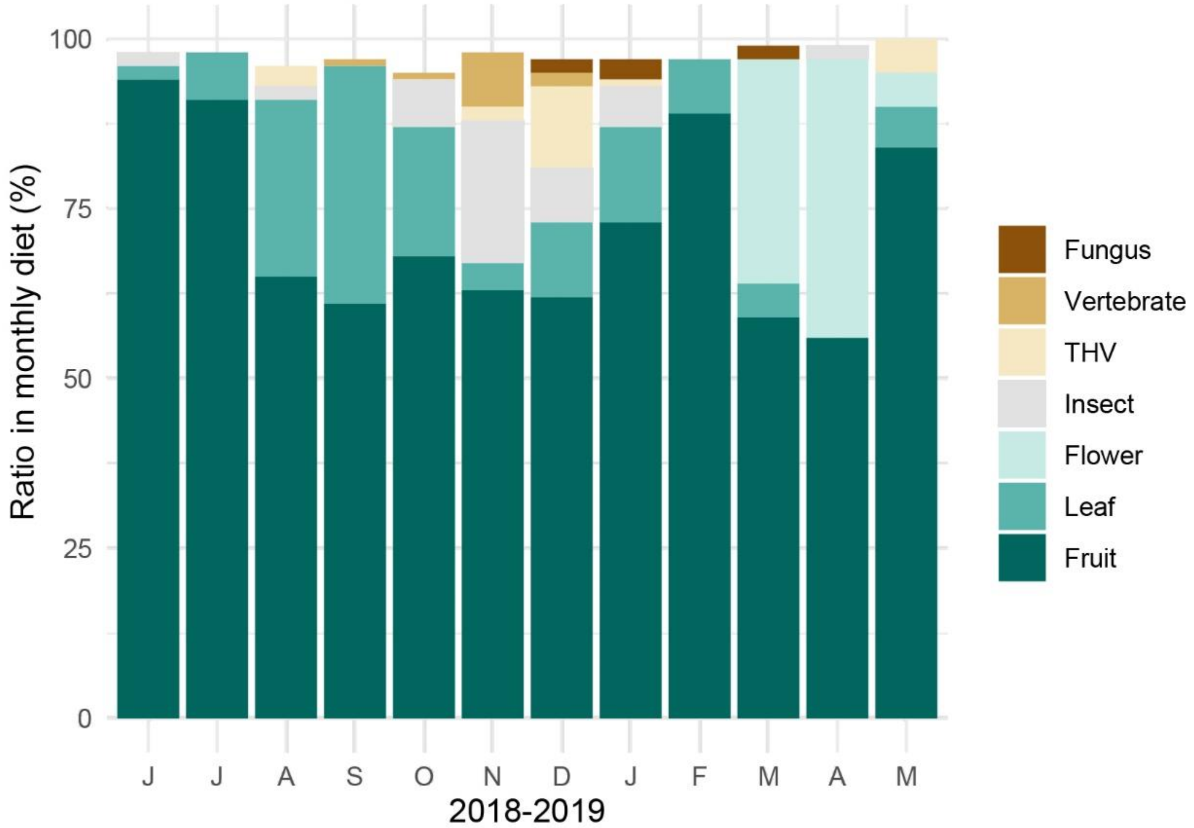


Figure 3.3 Monthly ratio of fruits, leaves, flowers, insects, terrestrial herbaceous vegetation (THV), vertebrates and fungus in Issa chimpanzee diet from June 2018 to May 2019

Table 3.4 Effect of season on the consumption of different food categories and important food items by Issa chimpanzees

Variable ~1 + sine (Julian date) + cosine (Julian date)		χ^2	P*
Categories	Fruit	5.750	0.310
	Leaf	**53.912**	**0.001**
	Flower	**249.210**	**< 0.001**
	Insect	**55.914**	**< 0.001**
	THV	7.042	0.576
	Vertebrate	**32.482**	**< 0.001**
	Fungus	**12.726**	**< 0.001**
Items	*Brachystegia spiciformis* leaf	103.750	**< 0.001**
	Cordia africana fruit	57.878	**< 0.001**
	Diplorhynchus condylocarpon fruit	100.940	**< 0.001**
	Englerophytum magalismontanum fruit	66.542	**< 0.001**
	Ficus spp. fruit	195.160	0.018
	Ficus spp. leaf	9.804	0.157
	Flacourtia indica fruit	65.711	**< 0.001**
	Garcinia huillensis fruit	262.450	**< 0.001**
	Julbernardia unijugata fruit	139.160	**< 0.001**
	Landolphia owariensis fruit	179.080	**< 0.001**
	Macrotermes subhyalinus termite	101.430	**< 0.001**
	Parinari curatellifolia fruit	59.753	**< 0.001**
	Pteridium aquilinum leaf	36.906	**< 0.001**
	Pterocarpus tinctorius flower	185.890	**< 0.001**
	Pterocarpus tinctorius leaf	36.238	**< 0.001**
	Saba comorensis fruit	105.910	**< 0.001**
	Strychnos sp. fruit	9.940	**< 0.001**
	Syzygium guineense fruit	124.250	**< 0.001**
	Uapaca nitida fruit	26.413	**< 0.001**
	Vitex doniana fruit	39.759	**< 0.001**
	Ximenia caffra fruit	15.381	**< 0.001**

* Degrees of freedom: 2, 12.

3.3. Preferred food items, fallback food items, and their nutritional values

Six items had a RPI < 0 and were thus identified as preferred foods (Table 3.3): fruits of *Ficus* spp., *G. huillensis, S. comorensis, F. indica* and *C. africana,* and flowers of *P. tinctorius*. There were no significant differences between preferred and non-preferred foods in macronutrient content relative to dry weight, except for fructose content, which was higher in preferred than in non preferred foods (W = 84, P = 0.004, Figure 3.4).

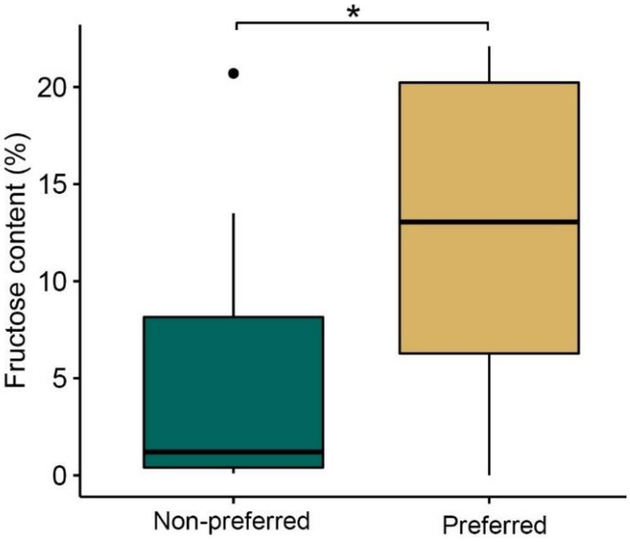


Figure 3.4 Fructose content (% of dry matter) was higher in Issa chimpanzees preferred foods than in non-preferred foods (*: significant difference, W = 84, P = 0.004)

Preferred food availability varied during the study period, and was the lowest in June–November 2018 and February–March 2019 (Figure 3.5).

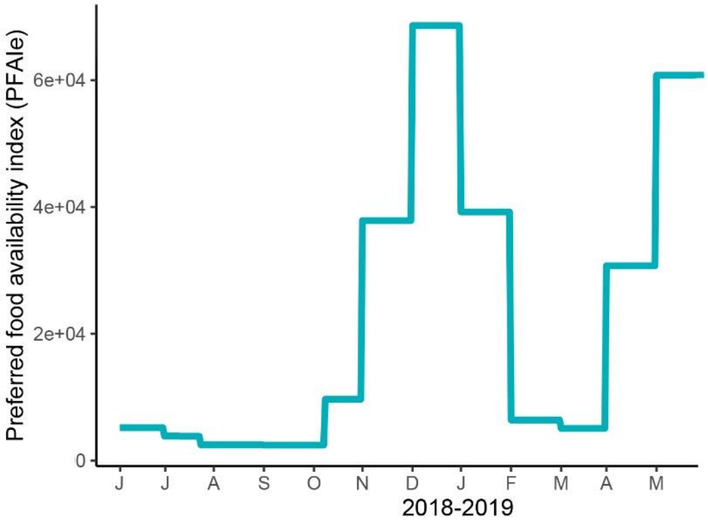


Figure 3.5 Preferred food availability index (PFAIe) for Issa chimpanzees from June 2018 to May 2019.

Only the consumption of leaves was negatively influenced by PFAIe; indicating that leaves were a fallback food for Issa chimpanzees during this period (Table 3.5, Figure 3.6). There was no significant correlations between PFAIe and consumption of THV, flowers, fungi, verterbrates, nor insects, indicating that these food categories are unlikely to be FBFs for Issa chimpanzees.

Table 3.5 Effect of preferred food availability index (PFAIe) on chimpanzee monthly leaf consumption

Term	Estimate ± SE	χ^2	P
(Intercept)	– 1.158 ± 0.312	–	–
Test predictors			
Preferred food availability index (PFAIe)[a]	– 0.008 ± 0.003	**24.047**	**0.007**
Control predictors			
Cosine (Julian date)	0.477 ± 0.306	**62.061[b]**	**< 0.001[b]**
Sine (Julian date)	– 1.165 ± 0.258		

n = 12 months. Statistically significant results (p<0.05) appear in bold.

[a] Square root transformed. Mean ± SD of the original variable: PFAIe: 23746 ± 23460

[b] Indicated is the overall test of the significance of season as obtained from comparing the full model with a reduced model lacking the two terms representing season.

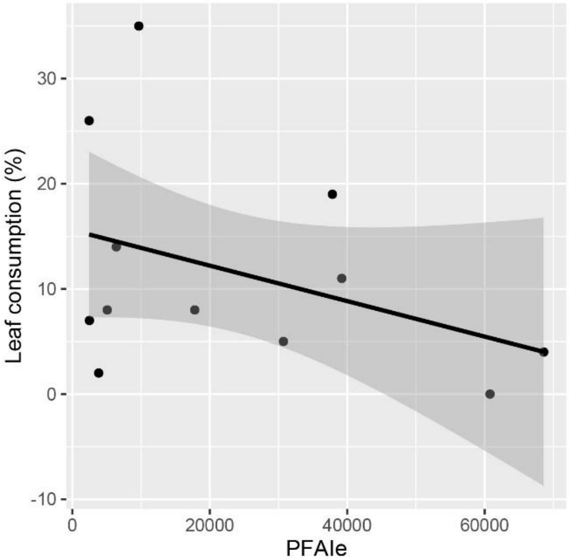


Figure 3.6 Correlation between percentage of leaf consumption in the diet and preferred food availability index (PFAIe) from June 2018 to May 2019; indicating that leaves were a fallback food for Issa chimpanzees during this period.

4. Discussion

4.1. Issa chimpanzee diet

During the study period, we observed Issa chimpanzees eating 70 plant food items from 48 plant species. This indicates less species variety than results from a previous study at Issa, primarily based on macroscopic analyses of fecal samples over five years, where 69 different plant species were recorded (Piel *et al.*, 2017). Thirty nine species were shared between the two studies and we found nine new species not previously described. This difference in diet breadth may reflect inter-annual differences in diet but more likely is a result of the recent habituation of Issa chimpanzees and the limited duration of the current study (*i.e.*, 1 year). If we combined results from fecal and direct observations, Issa chimpanzees would consume 78 plant species, which is higher than what was found at other savanna-woodland sites but lower than what has been reported elsewhere (except for 53 in Budongo, see Table 3.1. Environments with lower plant productivity such as high-altitude forest and savanna-woodland provide reduced plant food options, often resulting in lowered dietary breadth (Piel *et al.*, 2017; Matthews *et al.*, 2019). However, as these data are restricted to a single 12 mo period, it is too early to conclude that Issa chimpanzees have a narrower diet as a consequence of their potentially food-scarce habitat.

Consistent with all previous studies, Issa chimpanzee diet was dominated by fruit (72%). Among the fourteen important foods for Issa chimpanzees, eleven were fruits. Five of these fruit species (*i.e.*, *Ficus* spp., *S. comorensis, P. curatellifolia, F. indica* and *C. africana*) were also previously identified as important foods in Piel *et al.*'s (2017) diet study at Issa, and seven overlapped with important fruit species in the diet of a nearby forest-dwelling community of Gombe (Foerster *et al.*, 2016). I thus confirm Piel *et al.*'s finding that, despite dramatic differences in climate and plant diversity (Collins and McGrew, 1988), Issa chimpanzees generally choose similar fruit species as their forest-dwelling neighbors. Fruits are a valuable source of energy; they are rich in digestible carbohydrates, which are readily assimilated energy (Milton, 1993). Fruit represented 63% of the diet of Gombe chimpanzees (Wrangham, 1977), 65% for the Budongo chimpanzees (Newton-fisher, 1999), 64% for Kanyawara chimpanzees, and more than 80% of the Ngogo community diet (Potts *et al.*, 2009). In the only report from another dry habitat, Fongoli chimpanzees consumed fruit in 63% of feeding observations (Pruetz, 2006). The proprotion of fruit in diet seems to slightly vary across sites. It may be an illustration of chimpanzee ecology variability across its range but it may also likely be attributed to the discrepancy in the methodology used across sites (*e.g.*, continuous focal follow *versus* scans, inconsistent definition of fruits, *etc.*) and in the duration of the studies (Phillips and McGrew, 2014; Emery Thompson *et al.*, 2020).

Although they are fruit specialists, Issa chimpanzees consumed a diversity of food types from young leaves to flowers, THV, insects, fungi and meat. The third most important item in the annual diet during the study period was flowers of *P. tinctorius* (6% of the total diet) and the fourth *M. subhyalinus* termites (4% of the feeeding occasions). This expands the findings from the previous study on Issa chimpanzee's diet based on macroscopical fecal analyses, where flowers and insects could not be identified due to the limitations of this methodology (Piel *et al.*, 2017). All of the non-fruit food categories eaten by Issa chimpanzees are particularly rich in proteins. While fruits are an important source of energy in the form of digestible carbohydrates, they have lower levels of protein (Milton, 1993), and chimpanzees may need to complement their fruit-based diet with protein-rich foods (Milton, 1993). At Fongoli, for instance, chimpanzees are known to consume protein-rich termites (Bogart and Pruetz, 2011), and Taï chimpanzees derive a large amount of their dietary protein from nuts and hunted meat (Fahy *et al.*, 2013). Simarly, Issa chimpanzees selected leaves, flowers, THV, insects, fungi and meat probably in part for their high protein content. These results higlight that indirect methods as well as commonly used measures of food availability such as fruit availability index (that are exclusionary of non-fruit items), neglect some chimpanzee important foods.

Vertebrate meat was present in 1% of the total feeding occasions during the study period. The consumption of vertebrates is typical of all chimpanzee populations, with hunting frequency varying between sites and years but always representing a very small portion of the diet (Fisher, 2007). Although I could not measure the nutritional value of Issa chimpanzee's preys, they are likely to be highly nutritious and rich in proteins, fats and minerals (Stanford, 1996).

4.2. Seasonal variation in dietary composition

Leaves, flowers, insects, vertebrates, and fungi were consumed seasonally at Issa. For most of these categories, consumption seasonality likely paralleled similar patterns in availability. Young leaves are often produced seasonally in bursts (van Schaik *et al.*, 1993) and are typically preferred by chimpanzees over mature leaves because they have a lower fiber content (Milton, 1979). Leaf blooming often coincide with seasonal changes in weather and follows the months of maximum insolation (van Schaik *et al.*, 1993). At Issa, leaf consumption was the highest in August, September and October likely because they were highly available (see Chapter 2) during these last three months of the dry season. Similarly, fungi and flowers were mostly eaten when they were highly available (see Chapter 2), respectively during some months of the rainy season (December, January, March) and at the end of the rainy season (March–April). Termites were consumed at the beginning of the rainy season, from October to December, probably because during this period they increase construction activities, and many workers and soldiers come close to the surface making them more easily accessible for chimpanzees (McGrew *et al.*, 1979). During this period, chimpanzees use sticks to "fish" termites out of their underground tunnels (Teleki, 1974). Issa chimpanzees were seen hunting verterbrates only between August–December. During these months, food availability was at the highest (see Chapter 2), parties were very large (see Chapter 5), and daily travel distances were the highest recorded during the study period (see Chapter 4). Each of these three parameters (or a combination of them) could explain why Issa chimpanzees hunt more frequently during these months. First, hunting is energetically costy for chimpanzees (Tennie *et al.*, 2014) and thus may be reduced and/or absent when calorie intake is low. Second, catching preys sometimes requires group coordination, which may be facilitated when parties are larger (Boesch, 2002). Lastly, some authors argued that the probability of encountering prey is positively correlated with daily travel distance (*e.g.*, Gilby *et al.*, 2013), which increases during these months at Issa. All of this suggests that, although hunting at Issa is seasonal, it is likely opportunistic, and it counters the argument that hunting in savanna-woodland populations is necesarrily a response to seasonal increases in environmental pressures such as food scarcity (Linshield *et al.*, 2021)

The consumption of all food items followed a seasonal pattern, similar to other chimpanzee communities (Doran, 1997; Chancellor *et al.*, 2012; McLennan, 2013) except for *Ficus* spp. fruits and leaves. Species of the *Ficus* genus have a highly irregular fruiting pattern and individuals from the same species may fruit asynchronously several times a year (Leighton and Leighton, 1983). Figs were available throughout the year and Issa chimpanzees were observed eating them almost every month of the study period. Despite their unpredictable fruiting, and their poor nutritional quality compared to other fruits (low non-structural carbohydrates, low proteins and high crude fiber), figs are the most important feeding item in Issa chimpanzees diet, probably due to their availability throughout the whole year, making them a staple food for Issa chimpanzees.

4.3. Preferred foods

I found that six food items had a RPI<0 and were thus defined as preferred by Issa chimpanzees during the study period. I could not test whether fruits of *E. magalismontanum, L. owariensis* and *S. guineense* belonged to the preferred food category because I did not have phenological data for these species. Indeed, these species were not present in the phenological trails because their importance in Issa chimpanzee's diet was not known before this study. However, there are good indications to hypothesize that these items might be preferred foods, as Issa chimpanzees frequently fed on them when they were available (pers. obs). Furthermore, I could not quantify termite availability (or reachability by chimpanzees); however, we know that termites swarmed (Mitchell, 2007) at the beginning of the rainy season in the end of October toward beginning of December. During these months, chimpanzees were frequently observed fishing termites, which may indicate that termites are also a preferred food. I thus decided to consider these two fruits species and the termites as preferred food items as well. Contrary to my prediction not all preferred foods were fruits as flowers of *P. tinctorius* and termites were also preferred. The only nutritional difference I found between preferred and non-preferred foods was their content in fructose (also called fruit sugar), which was higher in the former. Non-structural carbohydrates (and particularly fructose), that provide readily assimilable energy (Milton, 1993), likely have an important role in Issa chimpanzees nutrition and may partially infuence their food choice.

Ficus spp. fruits are one of the most important preferred foods for Issa chimpanzees although they are nutritionally poor, given their high level of indigestible fiber and low level of non-structural carbohydrates and proteins. One advantage of figs is their low handling cost (Leighton, 1993) as they require no processing prior to be consumed, allowing chimpanzees to ingest more dry grams per minute when feeding on figs than when feeding on drupe fruit (Uwimbabazi *et al.*, 2019). Similar preference for figs has been described at Kahuzi-Biega (Yamagiwa and Basabose, 2009), Ngogo (Watts *et al.*, 2012a) and Nyungwe (Matthews *et al.*, 2019) although they were described as non-preferred at some other sites (Wrangham *et al.*, 1998; Furuichi *et al.*, 2001; Tweheyo *et al.*, 2004). Intersite variations in fig preference may be explained by the diversity, quality and seasonality of other feeding items (Wrangham *et al.*, 1993; Yamagiwa *et al.*, 1996). Habitats with lower overall food abundance and diversity in feeding item choices, such as savanna-woodlands or montane forests (Yamagiwa and Basabose, 2009; Matthews et al., 2019), may result in figs being relatively more preferred than in sites with richer feeding possibilities.

Termites are also likely to be a preferred food at Issa probably because they provide an opportunity for chimpanzees to obtain necessary, but rare protein, fats and minerals (Lieberman, 1987). At Gombe, researchers calculated that four hours of termite eating could yield up to 2 g of fat and close to 50 g of protein (O’Malley and Power, 2014). Furthermore, termite fishing is a stationary activity, requiring relatively little energy expenditure. During the periods when termites can be reliably fished, they can predictably meet or contribute to meeting a broad spectrum of nutrient and mineral requirements for Issa chimpanzees without requiring much energy expenditure while foraging.

Lastly, flowers of *Pterocarpus tinctorius* were a preferred food for Issa chimpanzees. They may be nutritionally profitable as they contain high levels of proteins while including also non-structural carbohydrates and lipids. Preferrence for flowers is not common for chimpanzees. At Budongo (Newton-fisher, 1999), Fongoli (Pruetz, 2006) and Nyungwe (Matthews *et al.*, 2019) flowers were also occasionally consumed at high rates but preference was not tested.

The preferrence for figs, flowers, and termites (among other items) at Issa broaden our knowledege of how flexible chimpanzee diet and feeding choices are across communities. Furthermore, the lack of clear distinction between preferred and non preferred items (except for fructose content) highlights that rather than selecting their preferred items based on specific macronutrient composition, Issa chimpanzees seem to choose each feeding item for a different reason (*e.g.*, fruits for their readily assimilable energy, leaves, insects and flowers for their protein content, figs for their ease in handling, *etc.*) and associate various items in their diet (depending on what is available) in order to get, through the easiest way possible, the variety of nutrients they require.

4.4. Fallback foods

Whereas some chimpanzee populations increase their consumption of THV (Wrangham *et al.*, 1993; Chancellor *et al.*, 2012), insects (Yamagiwa and Basabose, 2009) or figs (Wrangham *et al.*, 1998; Furuichi *et al.*, 2001) during lean periods, Issa chimpanzees used leaves as an important FBF. Leaves represented an important percentage of the feeding observations in August (26%) and September (35%, see Figure 3.3). Although we did not record the level of maturity of leaves during the feeding scans, we observed that leaves that were consumed in large amounts were the young leaves of *B. spiciformis* and *P. tinctorius* (pers. obs.), and availability of these leaves was highest in August and September when preferred foods were scarce (see Figure 3.5). Leaves are difficult to digest due to their high concentration in fiber and antifeedants, but they are good protein sources (particularly young leaves, Milton, 1979), and may also be valuable sources of metabolizable energy via hindgut fermentation (Milton, 1993). They contain high amounts of hemicellulose and cellulose, which are sources of energy for species capable of hindgut fermentation, such as chimpanzees (Conklin and Wrangham, 1994) and can be used when readily assimilable energy is not available. Leaves are regularly consumed in other chimpanzee communities suchs as Ngogo (Watts *et al.*, 2012), Sonso (Newton-Fisher, 1999), Kasekela (Wrangham, 1977) and Taï North (Anderson *et al.*, 2006) where they were also suggested to be FBFs although it was rarely tested.

Coping with dramatic fluctuations of food availability by including leaves into the diet could seem insuficient, in the first place, to fulfill individual energy requirements, although this is not the only adaptation that Issa chimpanzees implement during periods of food scarcity. They also reduce party size to minimize feeding competition (Chapter 5) and increase daily path length to find scarce but highly valuable feeding items (Chapter 4). These results highlight that particular items should not be generalized as preferred, non preferred, or FBFs for the chimpanzee species as these designations may depend on site-specific environmental productivity, botanical diversity and other behavioral strategies used to face resource scarcity.

Data on chimpanzee diet have implications for reconstructions of early hominins diet (*e.g.*, Stanford, 1996; Lucas *et al.*, 2008; Pruetz and Bertolani, 2009) and especially when it comes from populations living in savanna-woodlands. One of the challenges in paleoanthropology is to determine what foods could have met early hominin energetic needs (Nelson and Hamilton, 2017), particularly when moving into more open and seasonal landscapes (Cerling *et al.*, 2011). Paleoanthropologists can make inferences on the diet composition of our ancestors based on dental and cranial morphology, dental microwear, and more recently, stable isotope analyses (Scott *et al.*, 2005; Ungar, 2011; Cerling *et al.*, 2013). Dental microwear studies for instance, suggest that, similar to chimpanzees, early hominins such as australopithecines largely incorporated fruit in their diet (Teaford *et al.*, 2002) and may have thus been faced with very real energetic challenges as the availability of this resource became more scarce in both time and space (Blumenthal *et al.*, 2017). In this context, the FBFs used by early hominins would have played a central role in shaping these species' adaptations and evolution. Through early hominin evolution, premolars, molars, tooth enamel thickness and mandible size increased suggesting a diet increasing in hardness, abrasion, or toughness (Grine *et al.*, 2012). The exact nature of the FBFs to which these morphological adaptations corresponded remains uncertain (Knott, 2005) but it seems unlikely that these fallback resources were the same as those exploited by extant chimpanzees given the dental dissimilarities between the two genera (Lucas *et al.*, 2008). This highlights how early hominins may have adopted a different dietary strategy than chimpanzees when moving into more open and seasonal landscapes. Several researchers have suggested that USOs, such as roots, tubers, and rhizomes, may have been selected as FBFs by early hominins (Hatley and Kappelman, 1980; Wrangham *et al.*, 1999) and would have substantially increased the overall quality of the hominin diet compared to that of the chimpanzee's (Conklin-Brittain *et al.*, 2002). Authors then hypothesized that is possibly when hominins developed more effective means to face fluctuations in their food supply that they differentiated themselves from chimpanzee lineage (Knott, 2005). Although Hernandez-Aguilar *et al.* (2007) suggested that Issa chimpanzees may use tool to extract USOs based on indirect observations, the present study could not confirm this hypothesis. Studies of our closest living relatives inform us on the behavior that may have characterized our ancestors but also reveal the dissimilarities between the two genera. Our comprehension of what is unique to the human lineage continues to be redefined and challenged by what we learn about chimpanzees and especially populations that live in environments characterized by great variations in food availability.

By providing data from direct observations of a chimpanzee population living in a under-studied biome, the present study brings new insights into chimpanzee dietary responses to seasonal fluctuations in food availability, and into chimpanzee feeding ecology variability in general. Potential lower dietary breath, preference for figs, flowers and termites as well as periodic reliance on leaves from open-habitat-species illustrates some of the ways in which chimpanzee diet may respond to challenges associated with a savanna-woodland environment. While the present study mainly focused on describing qualitatively Issa chimpanzee diet, food choice and nutrient intake, subsequent studies should focus on determining the amount of nutrient and energy Issa chimpanzees get daily from the food they choose and how it varies temporally. Methods have been developped to estimate individual daily intake by coupling counts of the number of units eaten for each feeding item during full day focal follows with macronutrient analyses (Rothman *et al.*, 2011). This could allow to calculate a foraging (*i.e.*, searching, handling, extracting) time *versus* energy and nutrient gain ratio for each item and thus better understand Issa chimpanzees dietary choices. Additionally, future studies could focus on assessing temporal variations in Issa chimpanzees nutritional stress (Wessling *et al.*, 2018a) and on how it correlates with diet composition. This can be assessed through the measurement of C–peptide levels in urine samples (Emery Thompson *et al.*, 2009; Surbeck *et al.*, 2015) and could allow to evaluate more precisely the consequences of seasonal fluctuations in resource availability on individual physiological state and long term fitness. Finally, future intersite comparisons of chimpanzee morphological, physiological and genomic differences could investigate signatures that would facilitate certain macronutrients absorption through hindgut digestion, for instance (Lambert, 1998) at sites characterized by a high reliance on leaves (or other difficult to digest FBFs) such as Issa.

5. References

Altmann, J., 1974. Observational study of behavior: sampling methods. Behaviour. 49, 227–267.

Altmann, S.A., 1998. Foraging for Survival. University of Chigaco Press, Chicago.

Altmann, S.A., Altmann, J., 1970. Baboon Ecology: African Field Research. University of Chicago Press, Chicago.

Anderson, D.P., Nordheim, E. V., Boesch, C., 2006. Environmental factors influencing the seasonality of estrus in chimpanzees. Primates. 47, 43–50.

Aureli, F., Schaffner, C.M., Boesch, C., Bearder, S.K., Call, J., Chapman, C.A., Connor, R., Fiore, A.D., Dunbar, R.I.M., Henzi, S.P., Holekamp, K., Korstjens, A.H., Layton, R., Lee, P., Lehmann, J., Manson, J.H., Ramos-Fernandez, G., Strier, K.B., Schaik, C.P. van, 2008. Fission-Fusion Dynamics. Current Anthropology. 49, 627–654.

Basabose, A.K., 2002. Diet composition of chimpanzees inhabiting the montane forest of Kahuzi, Democratic Republic of Congo. American Journal of Primatology. 58, 1–21.

Blumenthal, S.A., Levin, N.E., Brown, F.H., Brugal, J., Chritz, K.L., Harris, J.M., Jehle, G.E., Cerling, T.E., 2017. Aridity and hominin environments. PNAS. 114, 7331–7336.

Boesch, C., 2002. Cooperative hunting roles among Taï chimpanzees. Human Nature. 13, 27–46.

Boesch, C., Bi, Z., Anderson, D.P., Stahl, D., 2006. Food choice in Taï chimpanzees: are cultural differences present? In: Hohmann, G., Robbins, M., Boesch, C. (Eds.), Feeding Ecology in Apes and Other Primates. Cambridge University Press, Cambridge, pp. 183–202.

Boesch, C., Boesch-Achermann, H., 2000. The Chimpanzees of the Taï Forest: Behavioural Ecology and Evolution. Oxford University Press., Oxford.

Boesch, C., Boesch, H., 1983. Optimisation of nut-cracking with natural hammers by wild chimpanzees. Behaviour. 26, 265–286.

Bogart, S.L., Pruetz, J.D., 2011. Insectivory of savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. American Journal of Physical Anthropology. 145, 11–20.

Bourliere, F., Hadley, M., 1983. Present-day savannas: an overview. In: Bourliere, F. (Ed.), Ecosystems of the World, 13, Tropical Savannas. Elsevier Scientific, Amsterdam, pp. 1–17.

Buckee, G.K., 1994. Determination of total nitrogen in barley, malt and beer by Kjeldahl procedures and the Dumas combustion method. Journal of the Institute of Brewing. 100, 57–64.

Cerling, T.E., Kyalo Manthi, F., Mbua, E.N., Leakey, L.N., Leakey, M.G., Leakey, R.E., Brown, F.H., Grine, F.E., Hart, J.A., Kaleme, P., Roche, H., Uno, K.T., Wood, B., 2013. Stable isotope-based diet reconstructions of Turkana Basin hominins. Proceedings of the National Academy of Sciences. 110, 10878–10878.

Cerling, T.E., Wynn, J.G., Andanje, S.A., Bird, M.I., Korir, D.K., Levin, N.E., Mace, W., Macharia, A.N., Quade, J., Remien, C.H., 2011. Woody cover and hominin environments in the past 6 million years. Nature. 476, 51–56.

Chancellor, R.L., Rundus, A.S., Nyandwi, S., 2012. The influence of seasonal variation on chimpanzee (*Pan troglodytes schweinfurthii*) fallback food consumption, nest group size, and habitat use in Gishwati, a montane rainforest fragment in Rwanda. International Journal of Primatology. 33, 115–133.

Chapman, C.A., Wrangham, R.W., Chapman, L.J., Kennard, D.K., Zanne, A.E., 1999. Fruit and flower phenology at two sites in Kibale National Park, Uganda. Journal of Tropical Ecology. 15, 189–211.

Chapman, C. A., Chapman, L. J., Rode, K. D., Hauck, E. M., & McDowell, L. R. 2003. Variation in the nutritional value of primate foods: Among trees, time periods, and areas. International Journal of Primatology, 24, 317–333.

Clutton-Brock, T.H., Harvey, P.H., 1977. Species differences in feeding and ranging behaviour in primates. In: Clutton-Brock, T.H. (Ed.), Primate Ecology: Studies of Feeding and Ranging Behavior in Lemurs, Monkeys, and Apes. Academic Press, London, pp. 557–584.

Collins, D.A., McGrew, W.C., 1988. Habitats of three groups of chimpanzees (*Pan troglodytes*) in western Tanzania compared. Journal of Human Evolution. 17, 553–574.

Conklin-Brittain, N. Lou, Wrangham, R.W., Hunt, K.D., 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. II. Macronutrients. International Journal of

Primatology. 19, 971–998.

Conklin-Brittain, N.L., Wrangham, R.W., Smith, C.C., 2002. A two-stage model ofincreased dietary quality in early hominid evolution: the role of fiber. In: Ungar, P.S., Teaford, M.F. (Eds.), Human Diet: Its Origin and Evolution. Bergin and Garvey, Westport, pp. 61–76.

Conklin, N.L., Wrangham, R.W., 1994. The value of figs to a hind-gut fermenting frugivore: A nutritional analysi. Biochemical Systematics and Ecology. 22, 137–151.

Doran, D., 1997. Influence of seasonality on activity patterns, feeding behavior, ranging, and grouping patterns in Taï chimpanzees. International Journal of Primatology. 18, 183–206.

Emery Thompson, M., Muller, M.N., Machanda, Z.P., Otali, E., Wrangham, R.W., 2020. The Kibale Chimpanzee Project : Over thirty years of research, conservation, and change. Biological Conservation. 252, 1–13.

Emery Thompson, M., Muller, M.N., Wrangham, R.W., Lwanga, J.S., Potts, K.B., 2009. Urinary C-peptide tracks seasonal and individual variation in energy balance in wild chimpanzees. Hormones and Behavior. 55, 299–305.

Emery Thompson, M., Wrangham, R.W., 2008. Diet and reproductive function in wild female chimpanzees (*Pan troglodytes schweinfurthii*) at Kibale National Park, Uganda. American Journal of Physical Anthropology. 135, 171–181.

Fahy, G.E., Richards, M., Riedel, J., Hublin, J., Boesch, C., 2013. Stable isotope evidence of meat eating and hunting specialization in adult male chimpanzees. PNAS. 110, 5829–5833.

Fisher, N.E.N., 2007. Chimpanzee hunting behavior. In: Henke, W., Tattersal, I. (Eds.), Handbook of Paleoanthropology. Springer Verlag, Berlin, pp. 1295–1320.

Foerster, S., Zhong, Y., Pintea, L., Murray, C.M., Wilson, M.L., Mjungu, D.C., Pusey, A.E., 2016. Feeding habitat quality and behavioral trade-offs in chimpanzees: A case for species distribution models. Behavioral Ecology. 27, 1004–1016.

Furuichi, T., Hashimoto, C., Tashiro, Y., 2001. Fruit availability and habitat use by chimpanzees in the Kalinzu Forest, Uganda: Examination of fallback foods. International Journal of Primatology. 22,

929–945.

Ganas, J., Robbins, M.M., 2005. Ranging behavior of the mountain gorillas (*Gorilla beringei beringei*) in Bwindi Impenetrable National Park, Uganda: A test of the ecological constraints model. Behavioral Ecology and Sociobiology. 58, 277–288.

Gilby, I.C., Pokempner, A.A., Wrangham, R.W., 2014. A direct comparison of scan and focal sampling methods for measuring wild chimpanzee feeding behaviour. Folia Primatologica. 81, 254–264.

Gilby, I.C., Wilson, M.L., Pusey, A.E., 2013. Ecology rather than psychology explains co-occurrence of predation and border patrols in male chimpanzees. Animal Behaviour. 86, 61–74.

Grine, F.E., Sponheimer, M., Ungar, P.S., Lee-Thorp, J., Teaford, M.F., 2012. Dental microwear and stable isotopes inform the paleoecology of extinct hominins. American Journal of Physical Anthropology. 317, 285–317.

Hamilton, W.J., 1985. Demographic consequences of a food and water shortage to desert chacma baboons, Papio ursinus. International Journal of Primatology. 6, 451–462.

Harrison, M.E., Marshall, A.J., 2011. Strategies for the use of fallback foods in apes. International Journal of Primatology. 32, 531–565.

Hatley, T., Kappelman, J., 1980. Bears, pigs, and Plio-Pleistocene hominids: a case for the exploitation of below ground food resources. Human Ecology. 8, 371–387.

Hemingway, C.A., Bynum, N., 2005. The influence of seasonality on primate diet and ranging. In: Brockman, D.K., van Schaik, C.P. (Eds.), Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates. Cambridge University Press, Cambridge, pp. 57–104.

Hernandez-Aguilar, R.A., Moore, J., Pickering, T.R., 2007. Savanna chimpanzees use tools to harvest the underground storage organs of plants. Proceedings of the National Academy of Sciences. 104, 19210–19213.

Hill, D.A., 1997. Seasonal variation in the feeding behavior and diet of Japanese Macaques (*Macaca fuscata yakui*) in lowland forest of Yakushima. American Journal of Primatology. 43, 305–322.

Isbell, L.A., 1991. Contest and scramble competition: Patterns of female aggression and ranging behavior among primates. Behavioral Ecology. 2, 143–155.

Isbell, L.A., Young, T.P., 1996. The evolution of bipedalism in hominids and reduced group size in chimpanzees: alternative responses to decreasing resource availability. Journal of Human Evolution. 30, 389–397.

Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology. 61, 65–71.

Knott, C.D., 2005. Energetic responses to food availability in the great apes : implications for hominin evolution, Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates. In: Brockman, D.K., van Schaik, C.P. (Eds), Cambridge University Press, Cambridge. pp. 351–378.

Lambert, J.E., 1998. Primate digestion: Interactions among anatomy, physiology and feeding ecology. Evolutionary Anthropology. 7, 8–20.

Lambert, J.E., 2007. Seasonality, fallback strategies, and natural selection: A chimpanzee *versus* cercopithecoid model for interpreting the evolution of hominin diet. Evolution of Human Diet: The Known, the Unknown, and the Unknowable. In: Ungar, P.S., (Ed.), Oxford University Press, Oxford, pp. 324–343.

Leighton, M., 1993. Modeling dietary selectivity by bornean orangutans : Evidence for integration of multiple criteria in fruit selection. International Journal of Primatology. 14, 257–313.

Leighton, M., Leighton, D., 1983. Vertebrate responses to fruiting seasonality within a Bornean rain forest. In: Sutton, S.L., Whitmore, T.C., Chadwick, A.C. (Eds.), Tropical Rain Forest: Ecology and Management. Blackwell Scientific Publications, Oxford, pp. 181–196.

Lieberman, L.S., 1987. Biocultural consequences of animals *versus* plants as sources of fats, proteins, and other nutrients. In: Harris, M., Ross, E.B. (Eds.), Food and Evolution: Towards a Theory of Human Food. Temple University Press, Philadelphia, pp. 225–258.

Lindshield, S., Hernandez-Aguilar, R.A., Korstjens, A.H., Marchant, L.F., Narat, V., Ndiaye, P.I., Ogawa, H., Piel, A.K., Pruetz, J.D., Stewart, F.A., van Leeuwen, K.L., Wessling, E.G., Yoshikawa, M., 2021. Chimpanzees (*Pan troglodytes*) in savanna landscapes. Evolutionary Anthropology.

Lucas, P.W., Constantino, P.J., Wood, B.A., 2008. Inferences regarding the diet of extinct hominins: Structural and functional trends in dental and mandibular morphology within the hominin clade. Journal of Anatomy. 212, 486–500.

Malenky, R.K., Wrangham, R.W., 1994. A quantitative comparison of terrestrial herbaceous food consumption by Pan paniscus in the Lomako Forest, Zaire, and *Pan troglodytes* in the Kibale Forest, Uganda. American Journal of Primatology. 32, 1–12.

Marshall, A.J., Boyko, C.M., Feilen, K.L., Boyko, R.H., Leighton, M., 2009. Defining fallback foods and assessing their importance in primate ecology and evolution. American Journal of Physical Anthropology. 140, 603–614.

Marshall, A.J., Wrangham, R.W., 2007. Evolutionary consequences of fallback foods. International Journal of Primatology. 28, 1219–1235.

Matsumoto-Oda, A., Kasagula, M.B., 2000. Preliminary study of feeding competition between baboons and chimpanzees in the Mahale Mountains National Park, Tanzania. African Primates. 21, 147–157.

Matthews, J.K., Grueter, C.C., Ridley, A., Kaplin, B.A., 2019. Chimpanzee feeding ecology and fallback food use in the montane forest of Nyungwe National Park, Rwanda. American Journal of Primatology. 81, 1–15.

McGrew, W.C., Baldwin, P.J., Tutin, C.E.G., 1988. Diet of wild chimpanzees (*Pan troglodytes verus*) at Mt. Assirik, Senegal: I. Composition. American Journal of Primatology. 16, 213–226.

McGrew, W.C., Tutin, C.E.G., Baldwin, P.J., 1979. Chimpanzees, tools, and termites : Cross-cultural comparisons of Senegal, Tanzania and Rio Muni. Man. 14, 185–214.

McLennan, M.R., 2013. Diet and feeding ecology of chimpanzees (*Pan troglodytes*) in Bulindi, Uganda: Foraging strategies at the forest–farm interface. International Journal of Primatology. 34, 585–614.

Milton, K., 1979. Factors influencing leaf choice by howler monkeys: A test of some hypotheses of food selection by generalist herbivores. The American Naturalist. 114, 362–378.

Milton, K., 1993. Diet and primate evolution. Science Advances. 269, 86–93.

Mitchell, J.D., 2007. Swarming and pairing in the fungus-growing termite, Macrotermes natalensis.

African Entomology. 15, 153–160.

National Research Council, 2003. Nutrient Requirements of Nonhuman Primates Second Revised Edition. The National Academies Press, Washington.

Nelson, S. V, Hamilton, M.I., 2017. Evolution of the human dietary niche. Initial transitions. In: Muller, M.N., Wrangham, R.W., Pilbeam, D. (Eds.), Chimpanzees and Human Evolution. Harvard University Press, Cambridge, pp. 311–338.

Newton-Fisher, N.E., 1999. The diet of chimpanzees in the Budongo Forest Reserve, Uganda. African Journal of Ecology. 37, 344–354.

Newton-Fisher, N.E., Reynolds, V., Plumptre, A.J., 2000. Food supply and chimpanzee (*Pan troglodytes schweinfurthii*) party size in the Budongo forest reserve, Uganda. International Journal of Primatology. 21, 613–628.

O'Malley, R.C., Power, M.L., 2014. The energetic and nutritional yields from insectivory for Kasekela chimpanzees. Journal of Human Evolution. 71, 46–58.

Ortmann, S., Bradley, B.J., 2006. Estimating the quality and composition of wild animal diets – a critical survey of methods. In: Hohmann, G., Robbins, M.M., Boesch, C. (Eds.), Feeding Ecology in Apes and Other Primates. Ecological, Physical and Behavioral Aspects. Cambridge University Press, Cambridge, pp. 395–418.

Phillips, C.A., McGrew, W.C., 2014. Macroscopic inspection of ape feces: What's in a quantification method? American Journal of Primatology. 76, 539–550.

Piel, A.K., Strampelli, P., Greathead, E., Hernandez-aguilar, R.A., Moore, J., Stewart, F.A., 2017. The diet of open-habitat chimpanzees (*Pan troglodytes schweinfurthii*) at Issa, Ugalla, western Tanzania. Journal of Human Evolution. 112, 57–69.

Potts, K.B., Chapman, C.A., Lwanga, J.S., 2009. Floristic heterogeneity between forested sites in Kibale National Park, Uganda : insights into the fine-scale determinants of density in a large-bodied frugivorous primate. Journal of Animal Ecology. 78, 1269–1277.

Potts, K.B., Watts, D.P., Wrangham, R.W., 2011. Comparative feeding ecology of two communities of chimpanzees (*Pan troglodytes*) in Kibale National Park, Uganda. International Journal of Primatology. 32, 669–690.

Pruetz, J.D., 2006. Feeding ecology of savanna chimpanzees. In: Hohmann, G., Robbins, M.M., Boesch, C. (Eds.), Feeding Ecology in Apes and Other Primates. Cambridge University Press, Cambridge, pp. 161–182.

Pruetz, J.D., Bertolani, P., 2009. Chimpanzee (*Pan troglodytes verus*) behavioral responses to stresses associated with living in a savannah-mosaic environment: Implications for hominin adaptations to open habitats. PaleoAnthropology. 252–262.

Reynolds, V., 2006. The Chimpanzees of Budongo. Oxford University Press, Oxford.

Richard, A.F., 1985. Primates in Nature. W.H. Freeman & Company, New York.

Rothman, J.M., Chapman, C.A., Soest, P.J. Van, 2011. Methods in primate nutritional ecology: A user's guide. International Journal of Primatology. 33, 542–566.

Schreier, B.M., Harcourt, A.H., Coppeto, S.A., Somi, M.F., 2009. Interspecific competition and niche separation in primates : A global analysis. Biotropica. 41, 283–291.

Scott, R.S., Ungar, P.S., Bergstrom, T.S., Brown, C.A., Grine, F.E., Teaford, M.F., Walker, A., 2005. Dental microwear texture analysis shows within-species diet variability in fossil hominins. Nature. 436, 693–695.

Sommer, V., Buba, U., Jesus, G., Pascual-Garrido, A., 2017. Sustained myrmecophagy in Nigerian chimpanzees: Preferred or fallback food? American Journal of Physical Anthropology. 162, 328–336.

Stanford, C.B., 1996. The hunting ecology of wild chimpanzees: Implications for the evolutionary ecology of pliocene hominids. American Anthropologist. 98, 96–113.

Stolwijk, A.M., Straatman, H., Zielhuis, G.A., 1999. Studying seasonality by using sine and cosine functions in regression analysis. Journal of Epidemiology and Community Health. 53, 235–238.

Stumpf, R., 2011. Chimpanzees and bonobos: inter and intraspecies diversity. In: Campbell, C.J., Fuentes, A., MacKinnon, K.C., Bearder, S.K., Stumpf, R.M. (Eds.), Primates in Perspective 2nd Edition.

Oxford University Press., Oxford, pp. 340–356.

Sugiyama, Y., Koman, J., 1992. The flora of Bossou: its utilization by chimpanzees and humans. African Study Monographs. 13, 127–169.

Surbeck, M., Deschner, T., Behringer, V., Hohmann, G., 2015. Urinary C-peptide levels in male bonobos (*Pan paniscus*) are related to party size and rank but not to mate competition. Hormones and Behavior. 71, 22–30.

Teaford, M.A., Ungar, P S, Grine, F.E., 2002. Paleontological evidence for the diets of African Plio-Pleistocene hominins with special reference to early Homo. In: Ungar, Peter S, Teaford, M.F. (Eds.), Human Diet: Its Origin and Evolution. Bergin and Garvey, Westport, pp. 143–166.

Teleki, G., 1974. Chimpanzee subsistence technology: Materials and skills. Journal of Human Evolution. 3, 575–594.

Tennie, C., Malley, R.C.O., Gilby, I.C., 2014. Why do chimpanzees hunt? Considering the benefits and costs of acquiring and consuming vertebrate *versus* invertebrate prey. Journal of Human Evolution. 71, 1–8.

Terborgh, J., Janson, C.H., 1986. The socioecology of primate groups. Annual Review of Ecology and Systematics. 17, 111–135.

Tutin, C.*E.G.*, Ham, R.M., White, L.J.T., Harrison, M.J.S., 1997. The primate community of the Lope Reserve, Gabon: Diets, responses to fruit scarcity, and effects on biomass. American Journal of Primatology. 42, 1–24.

Tweheyo, M., Lye, K.A., Weladji, R.B., 2004. Chimpanzee diet and habitat selection in the Budongo. Forest Ecology and Management. 188, 267–278.

Ungar, P.S., 2011. Dental Evidence for the Diets of Plio-Pleistocene Hominins. Yearbook of Physical Anthropology. 62, 47–62.

Uwimbabazi, M., Rothman, J.M., Basuta, G.I., Machanda, Z.P., Conklin-Brittain, N.L., Wrangham, R.W., 2019. Influence of fruit availability on macronutrient and energy intake by female chimpanzees. African Journal of Ecology. 1–12.

van Leeuwen, K.L., Hill, R.A., Korstjens, A.H., 2020. Classifying chimpanzee (*Pan troglodytes*) landscapes across large-scale environmental gradients in Africa. International Journal of Primatology. 41, 800–821.

van Schaik, C.P., Terborgh, J.W., Wright, S.J., 1993. The phenology of tropical forests : adaptive significance and consequences for primary consumers. Annual Review of Ecology and Systematics. 24, 353–377.

van Soest, P.J., 1994. The Nutritional Ecology of the Ruminant. Cornell University Press, Ithaca.

Wakefield, M.L., 2010. Socioecology of female chimpanzees (*Pan troglodytes schweinfurthii*) in the Kibale National Park, Uganda: Social relationships, association patterns, and costs and benefits of gregariousness in a fission-fusion society. Yale University.

Wallis, J., 2002. Seasonal aspects of reproduction and sexual behavior in two chimpanzee populations : a comparison of Gombe (Tanzania) and Budongo (Uganda). In: Boesch, C., Hohmann, G., Marchant, L.F. (Eds.), Behavioural Diversity in Chimpanzees and Bonobos. Cambridge University Press, Cambridge, pp. 181–191.

Watts, D.P., Potts, K.B., Lwanga, J.S., Mitani, J.C., 2012a. Diet of chimpanzees *(Pan troglodytes schweinfurthii*) at Ngogo, Kibale National Park, Uganda, 2. Temporal variation and fallback foods. American Journal of Primatology. 74, 130–144.

Watts, D.P., Potts, K.B., Lwanga, J.S., Mitani, J.C., 2012b. Diet of chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo, Kibale National Park, Uganda, 1. Diet composition and diversity. American Journal of Primatology. 74, 114–129.

Wessling, E.G., Deschner, T., Mundry, R., Pruetz, J.D., Wittig, R.M., Kühl, H.S., 2018a. Seasonal variation in physiology challenges the notion of Chimpanzees (*Pan troglodytes verus*) as a forest-adapted species. Frontiers in Ecology and Evolution. 6, 1–21.

Wessling, E.G., Dieguez, P., Llana, M., Pacheco, L., Pruetz, J.D., Kühl, H.S., 2020. Chimpanzee (*Pan troglodytes verus*) density and environmental gradients at their biogeographical range edge. International Journal of Primatology. 41, 822–848.

Wessling, E.G., Kühl, H.S., Mundry, R., Deschner, T., Pruetz, J.D., 2018b. The costs of living at the edge : Seasonal stress in wild savanna-dwelling chimpanzees. Journal of Human Evolution. 121, 1–11.

Wrangham, R.W., 1977. Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In: Clutton-Brock, T. (Ed.), Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes. Academic Press, pp. 503–538.

Wrangham, R.W., 1980. An ecological model of female-bonded primate groups. Behaviour. 75, 262–300.

Wrangham, R.W., Chapman, C.A., Clark-Arcadi, A.P., Isabirye-Basuta, G., 1996. Social ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups. In: McGrew, W.C., Marchant, L.F., Nishida, T. (Eds.), Great Ape Societies. Cambridge University Press, Cambridge, pp. 45–57.

Wrangham, R.W., Conklin-Brittain, N. Lou, Hunt, K.D., 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. International Journal of Primatology. 19, 949–970.

Wrangham, R.W., Conklin, N.L., Chapman, C. a, Hunt, K.D., 1991. The significance of fibrous foods for Kibale Forest chimpanzees. Philosophical transactions of the Royal Society of London. Series B. 334, 171–178.

Wrangham, R.W., Conklin, N.L., Etot, G., Obua, J., Hunt, K.D., Hauser, M.D., Clark, A.P., 1993. The value of figs to chimpanzees. International Journal of Primatology. 14, 243–256.

Wrangham, R.W., Jones, J.H., Laden, G., Pilbeam, D., Conklin-Brittain, N., 1999. The raw and the stolen: cooking and the ecology of human origins. Current Anthropology. 40, 567–594.

Yamagiwa, J., Basabose, A.K., 2009. Fallback foods and dietary partitioning among pan and gorilla. American Journal of Physical Anthropology. 140, 739–750.

Yamagiwa, J., Kaleme, K., Milinganyo, M., Basabose, K., 1996. Food density and ranging patterns of gorillas and chimpanzees in the Kahuzi-Biega National Park, Zaire. Tropics. 6, 65–77.

Yamakoshi, G., 1998. Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: Possible implications for ecological importance of tool use. American Journal of Physical Anthropology. 106, 283–295.

6. Appendix

Table 3.A.6 Monthly important food items (items that cumulatively comprise 75% of the monthly diet; listed by month in order of importance) for Issa chimpanzees.

2018–2019

	Jun	Jul	Aug	Sep	Oct	Nov
Imp food items (75% monthly diet)	*F.* spp. fruit	*F.* spp. fruit	*J.u.* fruit *B.s.* leaf *E.m.* fruit *P.c.* fruit	*F.* spp. fruit *B.s.* leaf *P.c.* fruit *E.m.* fruit	*S.c.* fruit *G.h.* fruit *M.s.* termite *P.c.* fruit *U.n.* fruit *P.t.* leaf *S.*sp. fruit X.c. fruit	*G.h.* fruit *M.s.* termite *S.c.* fruit

	Dec	Jan	Feb	Mar	Apr	May
Imp food items (75% monthly diet)	*G.h.* fruit *M.s.* termite *P.a.* leaf *S.c.* fruit	*S.g.* fruit *L.o.* fruit *F.* spp. fruit *F.* spp. leaf *G.h.* fruit	*F.* spp. fruit *L.o.* fruit	*F.* spp. fruit *P.t.* flower *D.c.* fruit	*P.t.* flower *F.* spp. fruit *F.i.* fruit *D.c.* fruit	*F.* spp. fruit *D.c.* fruit *C.a.* fruit *V.d.* fruit *F.i.* fruit

F. spp.*: Ficus sp, J.u.: Julbernardia unijugata, B.s.: Brachistegia spiciformis, E.m.: Englerophytum magalismontanum, P.c.: Parinari curatellifolia, S.c.: Saba comorensis, G.h.: Garcinia huillensis, M.s.: Macrotermes subhyalinus, U.n.: Uapaca nitida, S.*sp*: Strychnos sp; X.c.: Ximenia caffra, P.a.:Pteridium aquilinum, S.g.: Syzygium guineense, L.o.: Landolphia owariensis, P.t.: Pterocarpus tinctorius, D.c.: Diplorhynchus condylocarpon, F.i.: Flacourtia indica, C.a.: Cordia africana, V.d.: Vitex doniani*

Figure 3.A.7 Food samples from Issa chimpanzees reduced to a fine powder before energy and macronutrient analyses at IZW, Berlin

Figure 3.A.8 Energy assessment in food samples from Issa chimpanzees using an energy bomb calorimeter (C5003 bomb calorimeter; IKA–Werke GmbH & Co. KG, Staufen, Germany) at IZW, Berlin

Figure 3.A.9 Protein quantification in food samples from Issa chimpanzees via Dumas' combustion technique using a Rapid N III analyzer (Elementar Analyser Systeme GmbH, Hanau, Germany)

Figure 3.A.10 Carbohydrate quantification in food samples from Issa chimpanzees with commercialized enzymatic tests (R–Biopharm, Darmstadt, Germany; UV method) at IZW, Berlin

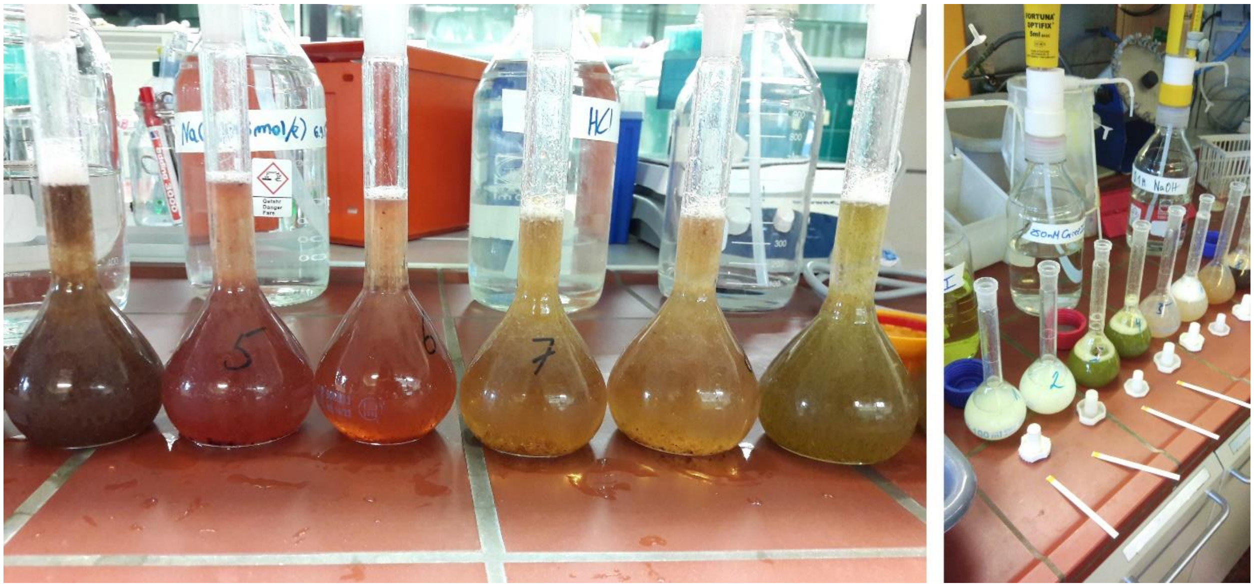


Figure 3.A.11 Carbohydrate quantification in food samples from Issa chimpanzees with commercialized enzymatic tests (R–Biopharm, Darmstadt, Germany; UV method) at IZW, Berlin

Figure 3.A.12 Fiber quantification in food samples from Issa chimpanzees via sequential digestion in petroleum ether-washed, sulfuric acid and sodium hydroxide at IZW, Berlin

Chapter 4: Resource availability and Issa chimpanzee ranging patterns.

To be submitted in summer 2022 to the International Journal of Primatology for publication

1. Introduction

Resource acquisition is a crucial part of all animals' lives and is a significant selective pressure affecting their biology and particularly their movements (Charnov, 1976). All foragers, including primates, tend to move across their environment in ways that optimize their energy (while also dealing with other aspects of their daily life such as minimizing their predation risk, interacting with conspecifics *etc*.) : they aim to consume the most nutritious foods available in their habitat while avoiding expending energy through unnecessary travel (Stephens and Krebs, 1986; Altmann, 1998). Dietary preferences influence habitat use (Clutton-Brock and Harvey, 1977). Folivores, for instance, forage within a smaller area than frugivores (Milton and May, 1976), as they mainly rely on relatively abundant leaves (Isbell, 1991). Alternatively, frugivores travel further to obtain ripe fruits, which are generally patchily distributed in space and time (Wrangham, 1980; Worman and Chapman, 2005) .

Resource availability changes seasonally in most primate habitats (van Schaik and Pfannes, 2005), and primates, especially frugivores, often face periods of resource scarcity (Clutton-Brock and Harvey, 1977). The consequences of insufficient resources are well documented among primates and include weight loss, hampered growth, reduced fecundity, and sometimes mortality (Hemingway and Bynum, 2005, Vogel *et al.*, 2012). Although physiological adaptations may support the maintenance of individuals during lean periods (*e.g.*, Canale *et al.*, 2011), many adaptations that allow individuals to limit the detrimental effects of resource scarcity are behavioral, such as ranging adaptations (Chapman *et al.*, 2012). In response to food source fluctuations, primates may adjust the size of the area within which they forage, switch habitat type, and/or adjust their traveling effort (Hemingway and Bynum, 2005). The distance individuals travel each day is referred to as their day range or daily path length (DPL) and the area they utilize is called their home range (HR). In response to resource scarcity, optimal foraging theory predicts that individuals may either adopt an energy maximizing strategy by increasing travel effort (*i.e.*, increasing DPL) to access high quality resources or they may reduce energy spent on travel (*i.e.*, reduce DPL) and switch to more accessible but lower quality foods (Stephens and Krebs, 1986). Some species such as baboons (*Papio ursinus*: Pebsworth *et al.*, 2012, *P. anubis*: Harding, 1976), gorillas (*Gorilla* *beringei beringei:* Ganas and Robbins, 2005), or lemurs (*Eulemur fulvus rufus:* Overdorff, 1996), adopt an energy maximizing strategy whereby they increase their DPL during the lean season, whereas others such as gibbons (*Nomascus concolor jingdongensis*: Fan and Jiang, 2008) and chimpanzees *(Pan troglodytes*: Doran, 1997; Herbinger *et al.*, 2001; Matsumoto-Oda, 2002; N'guessan *et al.*, 2009; Moore et al., 2018; Green *et al.*, 2020) reduce DPL as a response to resource scarcity. DPL adjustments are generally associated with temporary changes in HR size (Van Schaik *et al.*, 1993). Primates also change locations by moving among habitats and occasionally out of their "regular" HR in search of more resource-rich areas (*e.g.*, increase use of swamps: Stevenson *et al.*, 1994; Defler, 1996; Poulson *et al.*, 2001). These ranging strategies are often coupled with dietary adjustments where individuals switch towards consuming more abundant and accessible, lower-quality fallback foods (Charnov, 1976).

Whereas there is a wealth of data from studies that address the role of food availability on primate ranging behavior, water is less commonly considered as a driver of movement patterns. All primates require drinking water to survive, but water can be extremely limited and patchily distributed during the dry season in some regions (Altmann and Altmann, 1970). Waterholes have been shown to influence patterns of habitat use and movement in olive baboons (Barton *et al.*, 1992), red-fronted lemurs (*Eulemur rufifrons:* Scholz and Kappeler, 2004), white-faced capuchins (*Cebus capucinus:* Campos and Fedigan, 2009), and chacma baboons (Noser and Byrne, 2014). Specifically, individuals decrease their DPL when surface water becomes scarce and they center their movements and activity around the remaining permanent water sources (Campos and Fedigan, 2009).

Despite the increased awareness of ecological variability at the species level (Strier, 2009), we generally lack sufficient information on the factors that drive within-species variation in primate ranging patterns. Understanding these factors is particularly important for species living in ecologically heterogenous environments with high spatial and temporal variability, because these conditions often lead to pronounced fluctuations in resource availability (Hemingway and Bynum, 2005). An appropriate species in which to investigate the responses to these conditions is the chimpanzee. Chimpanzees live across a diverse ecological gradient from closed canopy forest to open savanna-woodlands (van Leeuwen *et al.*, 2020) and thus face varying biotic and abiotic conditions. Chimpanzees are large-bodied, ripe-fruit specialists that depend on widely dispersed food patches imposing long day ranges, *i.e.*, means of 2–5 km (Gombe, Tanzania: Wrangham, 1977; Mahale, Tanzania: Hunt, 1989; Taï, Ivory Coast: Herbinger *et al.*, 2001; Kibale, Uganda: Pontzer and Wrangham, 2004). Chimpanzee HRs typically fall between 6 and 37 km^2 (Amsler, 2009). Chimpanzee ranging is affected by various ecological factors, including the distribution and availability of resources (Bertolani, 2013). Chimpanzees decreased their DPL in periods of low food availability at various sites (Gombe: Wrangham, 1977; Mahale: Matsumoto-Oda, 2002; Taï, Ivory Coast: Doran, 1997; Herbinger *et al.*, 2001; N'guessan *et al.*, 2009; Nyungwe, Rwanda: Green *et al.*, 2020); however, to date, no study has looked at the impact of water availability on chimpanzee DPL.

While all the studies presented here come from forest communities, relatively little is known about the ranging ecology of chimpanzees living in savanna-woodland landscapes. Savanna-woodland environments have lower tree density than continuous forests (Crowther *et al.*, 2015), resulting in more scarce and patchily distributed resources. These characteristics suggest that chimpanzees living in these landscapes may increase their DPL and may thus have larger HRs than those of forest-dwelling chimpanzees (Kano, 1971; Baldwin *et al.*, 1982; Moore, 1992; Pruetz and Bertolani, 2009). To date, HR figures for savanna-woodlands have been reported mostly from unhabituated (or partially habituated) communities (Table 4.1), but because for unhabituated communities, researchers used indirect methods (based on nests counts and density) to estimate HR, these estimations are less likely to be precise. The only HR estimate from an habituated savanna-woodland community comes from Fongoli, Senegal: approximatively 90 km^2 (Pruetz and Herzog, 2017), but the method used was not indicated in the study. Savanna-woodlands are considerably more seasonal than forested habitats (Alberts *et al.*, 2005; Piel *et al.*, 2017), with periods of resource scarcity leading to potentially greater seasonal variations in ranging patterns. Additionally, they are highly heterogenous environments, as they consist of both forest and non-forest areas that host different types of vegetation based on varying soil characteristics and distribution of surface and groundwater (Duvall, 2011).

Table 4.1 Comparison of wild chimpanzee communities' home range (HR) sizes

Community	Hab	HR (km^2)	Method	Source
Assirik	SW	470–560	Inference from density based on nest count	Baldwin *et al.*, (1982)
		72.1	MCP	Hunt and McGrew, (2002)
Bossou	F	15	MCP	Koops, (2011)
Budongo (Sonso)	F	6.78	MCP	Newton-Fisher, (2003)
		6.89	Fixed kernel	
		9.71	MCP	Fawcett, (2000)
		9.19	Fixed kernel	
		18.21	Adaptive kernel	
Fongoli	SW	63	MCP based on nest count	Pruetz, (2006)
		85	unknown	Skinner and Pruetz, (2012)
Gombe	F	13	500 × 500-m grid cell	Wrangham, (1979)
		5.4	MCP	Williams *et al.*, (2002)
Issa	SW	36	MCP	this study
		30.3	500 × 500-m grid cell	
Kahuzi-Biega	F	7.6	250 × 250-m grid cell	Basabose, (2005)
Kasakati	SW	201	Inference from density based on nest count	Suzuki, (1969)
		120	Inference from density based on nest count	Izawa, (1970)
Kibale (Kanyawara)	F	14.9	MCP	Chapman and Wrangham, (1993)
		8.5	200 × 200-m grid cell	
		37.8	MCP	Wilson, (2001)
Kibale (Ngogo)	F	28.76	MCP	Mitani *et al.*, (2010)
Mahale (K-Group)	F	6.2	MCP	Nishida and Hiraiwa-Hasegawa, (1987)
Mahale (M-Group)	F	19.4	MCP	Nishida and Hiraiwa-Hasegawa, (1987)
		18.4	MCP	Nakamura *et al.*, (2013)
Nyungwe	F	40	MCP	Green *et al.*, (2020)
Semliki (Mugiri)	SW	50.1	MCP	Hunt and McGrew, (2002)
Seringbara (Guinea)	F	20	MCP	Koops, (2011)
Taï (North)	F	16.5–26.9	MCP	Boesch and Boesch-Achermann, (2000)
		13.9–26.4	MCP	Lehmann and Boesch, (2003)
		16.8	MCP	Herbinger *et al.*, (2001)
		18.3	500 × 500-m grid cell	
Taï (Middle)	F	12.1	MCP	Herbinger *et al.*, (2001)
		13	500 × 500-m grid cell	
Taï (South)	F	26.5	MCP	Herbinger *et al.*, (2001)
		23.3	500 × 500-m grid cell	
Ugalla	SW	470–560	Inference from density based on nest count	Kano, (1971)
		700–750	Inference from density based on nest count	Itani, (1979)
		470–500	Inference from density based on nest count	Ogawa *et al.*, (2007)

Hab: habitat, SW: savanna-woodland, F: forest, MCP: minimum convex polygon, GC: grid cell

Vegetation heterogeneity offers a time-dispersed production in chimpanzee food items as biotic and abiotic factors shift throughout the year and influence distinctively each plant species' productivity (Watts *et al.*, 2012). During periods of food scarcity, chimpanzees may exploit this heterogeneity and switch habitat. For instance, grey-cheeked mangabey (*Lophocebus albigena*) increased their use of swamp habitats when food availability decreased (Poulson et al., 2001). Chapter 3 revealed that some woodland species were consumed more frequently during the food-scarce period, likely resulting in a greater use of this habitat at this time of the year. Finally, savanna-woodlands impose considerable hydration pressure on chimpanzees (Wessling *et al.*, 2018) and may in turn influence ranging patterns, especially during water-scarce periods (Lindshield *et al.*, 2021). Chimpanzees need to drink every day in the dry season because they cannot survive on metabolic water (McGrew *et al.*, 1981), but water may be seasonally hard to find in these landscapes (Moore, 1996). This could result in individuals ranging over larger areas to locate permanent water, or else restrict ranging to natural springs. Preliminary results at Fongoli indicated a shift in habitat use between dry *versus* wet season when chimpanzees relied on a single spring (Pruetz and Bertolani, 2009), but there were no data reported on DPL or the impact of shifting water or food availability on ranging/DPL. As such, we are still lacking data on ranging patterns responses to variations in resource availability in drier habitats (Lindshield *et al.*, 2021). Studying chimpanzee ranging patterns in an understudied biome, characterized by high environmental variability, provides insight on the species' behavioral diversity across its range and may reveal adaptations not observed elsewhere (Kalan *et al.*, 2020) .

Moreover, comparisons of chimpanzee ranging patterns between different habitats can inform on the environmental pressures that may have shaped the ranging behavior of early hominins. Given their morphological, physiological and genetic similarities to humans (Cheng *et al.*, 2005), chimpanzees have been argued by some authors to represent our best living analogue of early human behavior (Muller *et al.*, 2017). Hominin evolution is characterized by adaptations to environmental shifts from closed, homogeneous forests to drier, more heterogeneous open landscapes (White *et al.*, 2009; Cerling *et al.*, 2011; Potts, 2013). These open, savanna-woodland environments were drier (Bromage and Schrenk, 1995; Potts, 1998; Passey *et al.*, 2010), more seasonal (Foley, 1993), characterized by a less abundant distribution of food (Isbell and Young, 1996), and very similar to some current chimpanzee habitats, such as the savanna-woodland of Issa (Hernandez-Aguilar, 2009). As such, studying ranging patterns of one of our closest living relatives inhabiting these extant savanna-woodlands brings the opportunity to better understand the environmental pressures under which hominins lived and the ranging responses that might have been involved in adaptations to these « new » environments (Moore, 1996).

Chimpanzee ranging patterns are described from a limited part of their distribution and no study has yet examined how ranging behavior and resource availability interact in a dry habitat. In addition to being similar to paleoenvironments, savanna-woodland landscapes are often deemed marginal for chimpanzees because of their distinct ecological challenges (*e.g.*, dehydration, low fruit abundance, vegetative heterogeneity, and high seasonality) that may elicit particular ranging responses. The Issa valley in western Tanzania, defined as a savanna-woodland landscape, hosts a previously unstudied population of chimpanzees, and offers the opportunity to evaluate how resource availability shapes chimpanzee ranging patterns in this landscape. I sought to address four questions in the present study: do Issa chimpanzees (1) shift their range throughout the year?

(2) adjust their DPL to variations in resources availability?

(3) modify their habitat use in response to resource availability?

I expected HR to be larger than what is found at other sites given the potential lower food availability associated with the Issa savanna-woodland landscape. I expected DPL to decrease when food is scarce as it is the case in other chimpanzee communities; and I expected water scarcity to limit DPL because chimpanzees would need to stay close to water sources. I expected Issa chimpanzees to spend more time in open woodland areas during food-scarce season (because these areas would be richer in fallback foods), and to stay in evergreen patches of forests during periods of water scarcity because these patches host perennial water.

2. Material and methods

2.1. Data collection

Climate data

Rainfall data were recorded at 30-min intervals using an electronic rain gauge (Onset Corp., HOBO, model RH3, precision 2 mm) placed at the base camp located within the Issa community's HR.

Food availability

I calculated a food availability index based on the ten most important plant food items in the Issa diet (see Chapter 2) using the following formula:

$$FAIe_m = \sum_{1}^{10} P_{ism} \times BA_{si} \times M_i \times E_i$$

where P_{im} denotes the mean abundance of item *i* on species *s* in month *m*, BA_{si} represents the basal area per hectare in Issa area for the species *s* to which the item *i* belongs, M_i represents the average dry mass for item *i* and E_i represents the average energy per gram of dry mass for item *i*.

Water availability

I calculated a water availability index (WAI) following Wessling *et al.* (2018) (see Chapter 2) using the following equation:

$$WAI_m = \sum_{1}^{8} \frac{Depth_{im}}{Depth_{\max[i]}}$$

where ($Depth_{im}$) denotes the depth of source *i* for month *m* and $Depth_{max[i]}$ the maximum observed depth for source *i*. WAI ranges from zero (no ground water available) to one (maximum water available).

Behavioral observations

Focal follows (Altmann, 1974) of eight adult chimpanzees were attempted approximately 20 days per month from June 2018 to May 2019. An assistant or I randomly chose a focal individual from the first party encountered and followed the focal individual for as long as possible, ideally until s/he built their night nest. Focal chimpanzee locations were recorded at 5-minute intervals using the GNSS receiver of an Android tablet (CUBOT MTK6753A).. We also recorded habitat structure: open (comprised of woodland, and swamps) and closed (riparian evergreen forest) for each point. If the target individual was lost during a follow, every attempt was made to regain contact, but if this was not possible within 30 minutes, we selected a new individual to follow. GPS accuracy was within 10 m throughout most of Issa HR.

2.2. Data analysis

Home range

In order to provide estimates that would be comparable with those of other studies, I used two methods to estimate HR size (see Appendix, Figure 4.A.5): the minimum convex polygon (MCP) method and the grid cell (GC) method. Calculating MCP involves creating a polygon around data points with convex angles only (Hayne, 1949). Although the MCP method has shortcomings, such as sensitivity to outliers and to sample size, it makes no assumptions regarding the independence of observations, and it is statistically stable (Jennrich and Turner, 1969). Moreover, it has been widely used in similar, previous studies, and thus will allow for inter-population comparisons (see Table 4.1). GC is another widely used method, involving a superimposed grid with a mesh of a chosen size over the area in which evidence of a community is found. In contrast to MCP, the GC method is not sensitive to outliers and does not include areas that are not used within the HR polygon. For MCP analysis, I created a polygon around all observation points using the "Minimum bounding geometry" tool and calculated the area of the polygone in QGIS (version 3.12 – Bucaresti, QGIS Development Team 2020). For the GC method I superimposed a grid over a rectangle that encompassed all observations made during the study period in QGIS. I used 500 × 500 m grid cells to align with other chimpanzee studies (Herbinger *et al.*, 2001; Lehmann and Boesch, 2005; Amsler, 2009). I calculated home range size by multiplying the sum of cells in which chimpanzee observations were made by the area of a single cell, *i.e.*, 0.25 km^2 (Chapman and Wrangham, 1993). HR size at Issa was estimated using all observation points collected during the study period and I estimated monthly ranges using observations points collected during each month.

Travel paths

I created daily paths by joining each consecutive way-point with a straight-line segment in QGIS (see Appendix, Figure 4.A.6). Only focal follows ≥ five hours were used for this analysis (Doran, 1997). I calculated the distance traveled by summing the distances between consecutive 5-min way-points. I divided this value by the total focal daily observation time to obtain an approximate distance traveled per hour and to estimate total daily path length (DPL), I multiplied this value by 12 hours (Lehmann and Boesch, 2004).

2.3. Statistical analysis

I performed all statistical analyses in the statistical program R v. 3.4.0 (R Core Team, 2017) and set the significance level alpha at 0.05.

DPL model

I examined the influence of food and water availability on distance traveled per day using a linear mixed effects model with a Gaussian error structure and identity link function. I modelled daily individual DPL as the dependent variable; fixed effects were monthly FAIe and monthly WAI. I also included control predictors in the model, *i.e.*, variables that are likely to have an impact on the dependent variable but that are not related to my research questions. I included mean daily party size of the focal individual as a control predictor because among primates that exhibit fission-fusion, party size is known to have a positive impact on DPL (Clutton-Brock and Harvey, 1977; Chapman *et al.*, 1995). I included sex of the focal individual as a control predictor because male chimpanzees are known to travel more than females (Chapman and Wrangham, 1993; Williams *et al.*, 2002; Bates and Byrne, 2009). To account for seasonality in DPL, I included a seasonal term as a control predictor represented by both sine and cosine of Julian date (divided by 365.25 and then multiplied by 2π) (Stolwijk *et al.*, 1999; Wessling *et al.*, 2018). This seasonal term assumes regular periodicity in a single annual cycle. Follow duration was included as a control predictor. Daily rainfall was also included as a control predictor variable because primates often stopped travelling during heavy rain, and a negative correlation between DPL and rainfall has already been reported in other primates species (*e.g.*, gorillas: Ganas and Robbins, 2005). I also included follow duration as a control predictor. Finally, to account for certain individuals having a disproportionate effect on the dependent variable, the identity of the focal chimpanzee was included as a random effect.

Habitat model

To test the influence of food and water availability on habitat use, I used a linear mixed effects model with a binomial error structure and logit link function. We used a binomial error structure because the dependent variable (*i.e.*, habitat structure) has a binary outcome (*i.e.*, open or close). The habitat structure for each 5-minute scan was modelled as the dependent variable and fixed effects were monthly FAIe and monthly WAI. I included the seasonal term described previously as a control predictor. I also included rainfall at the time of the scan as a control predictor variable in case chimpanzees sought refuge under thicker canopy during heavy rain. I included sex of the individual and time of the day as control predictors. As above, the identity of the focal chimpanzee was included as a random effect. Because consecutive scans were likely to occur under more similar social or ecological conditions, the response variable (habitat structure) was likely to show temporal autocorrelation unexplained by the fixed effects included in the model. This may lead to the violation of the assumption of independent residuals (*i.e.*, neighboring residuals being more similar than more distant ones) devaluating the reliability of the model. Therefore, I incorporated temporal autocorrelation into the habitat model as described in Furtbauer *et al.*, (2011) by first running the model as described above. I retrieved the residuals from that model and calculated a temporal autocorrelation term for each data point, which was the weighted mean of all other residuals, with the weight equaling the inverse number of days between respective data points and the residual. The weighting function followed a normal distribution. I then included the "autocorrelation term" as an additional control factor into the model.

Checking model assumptions

For both models, I checked for the assumptions of normally distributed and homogenous residuals by visually inspecting Q–Q plots and the residuals plotted against fitted values and found no violations. I checked for model stability by excluding each level of the random effect one at a time and comparing the estimates derived from these datasets with those derived for the full dataset and found that the models were sufficiently stable. Variance inflation factors were derived using the 'vif' function of the 'car' package (Fox and Weisberg, 2011) based on a standard linear model excluding random effect, and no collinearity issues were found. Before interpreting the results of the models, I first determined the significance of the full models (including all predictors and random effects) as compared to the corresponding null models (including only the control predictors and the random effects) with a likelihood ratio test (Dobson, 2002) using the R function ‘anova’. I measured the impact of each predictor using likelihood ratio tests comparing the full models with respective reduced models (full models without the predictors).

3. Results

3.1. Issa home range

I collected data on 13,472 individual locations. The MCP method yielded a larger estimated HR size, *i.e.*, 36 km^2 than the GC (500 m × 500 m) method, *i.e.*, 30.3km^2 (Figure 4.1).

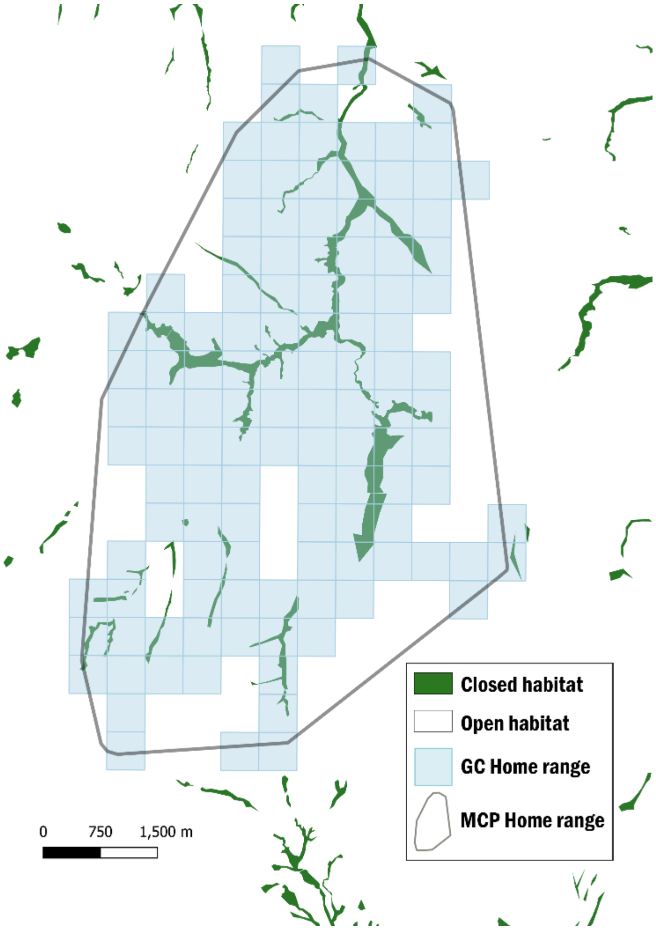
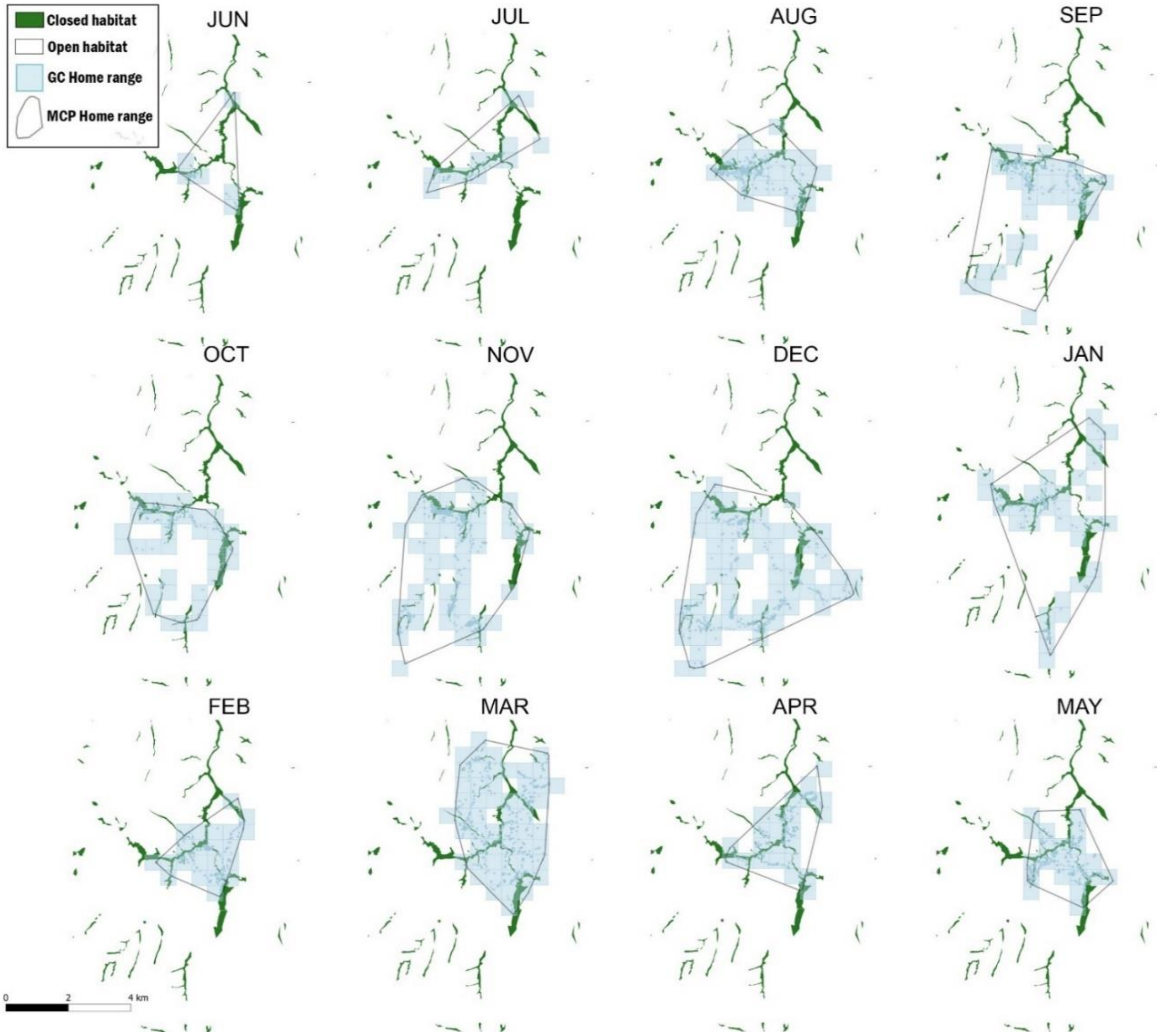


Figure 4.1 Issa chimpanzees home range (June 2018–May 2019) calculated using two different methods: minimum convex polygon (MCP; 36km2), and grid cell 500 m × 500 m (GC; 30.3km2).

I observed monthly shifts in range use (Figure 4.2). For instance, September and March ranges were very different with only 10.2% of overlap between these two months.

The Issa chimpanzee HR was larger than most other communities for which data are available (Table 4.1).



June, *n*=404; July, *n*=655; August, *n*=1143; September, *n*=911; October, *n*=374; November, *n*=1111; December, *n*=965; January, *n*=621; February, *n*=575; March, *n*=1634; April, *n*=760; May, *n*=1029 data points.

Figure 4.2 Issa chimpanzees monthly ranges calculated using two different methods: minimum convex polygon, and grid cell 500 m × 500 m during the study period (June 2018-May 2019).

3.2. Daily path length model

I obtained 144 daily path lengths across 109 days of follows. Average DPL was 3.32 ± 2.14 km. The DPL full–null model comparison was significant (likelihood ratio test: χ^2 = 10.698, df =3, P = 0.013), indicating that DPL increased with decreasing food availability, but was not influenced by water availability (Table 4.2).

Table 4.2 GLMM testing the effect of monthly food availability index (FAIe), monthly water availability index (WAI) and party size on focal individual daily path length (DPL).

Term	Coded level	Estimate ± SE	χ2	P
(Intercept)		2.446 ± 0.453	–	–
Test predictors				
Food availability index (FAIe)[a]		**– 0.612 ± 0.287**	**4.657**	**0.031**
Water availability index[a]		– 0.453 ± 0.531	0.847	0.357
Control predictors				
Cosine (Julian date)		**1.563 ± 0.421**	**14.285[b]**	**< 0.001[b]**
Sine (Julian date)		**0.416 ± 0.726**		
Party size[a]		**0.384 ± 0.188**	**3.963**	**0.047**
Sex[c]	Male	0.971 ± 0.523	3.535	0.060
Daily rainfall[a]		– 0.300 ± 0.187	2.945	0.086
Follow duration[a]		– 0.281 ± 0.172	1.942	0.163

n= 144 ≥ 5H-follows. Statistically significant results (p ≤ 0.05) appear in bold.
Focal ID (n=8) was included as random factor.
[a] Z-transformed to a mean of 0 and a standard deviation of 1. Original means ± SD of the original variable: FAIe: 524654.4 ± 486975.6; WAI: 0.58 ± 0.25; party size 7.90 ± 3.98; rainfall 3.70 ± 8.09, follow duration 8.81 ± 2.13.
[b] Indicated is the overall test of the significance of season as obtained from comparing the full model with a reduced model lacking the two terms representing season.
[c] Estimate refers to the comparison with the reference category: Female.

Relatedly, I found that DPL was highly seasonal (Figure 4.3) and increased with party size (Table 4.2, see Chapter 5 for insights into temporal fluctuations in party size at Issa).

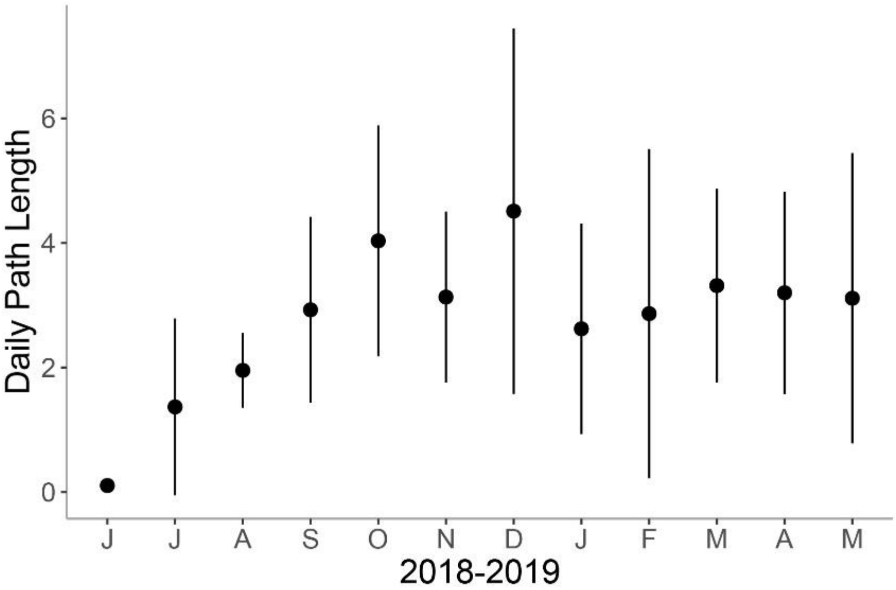


Figure 4.3 Issa chimpanzee monthly daily path length (DPL, in km) during the study period

3.3. Habitat use model

Issa chimpanzees spent 53% of their time in open habitat on average, but dramatic monthly variations occurred with a minimum of 12% in June 2018 and a maximum of 93% in March 2019 (Figure 4.4).

The habitat full-null model comparison was not significant (likelihood ratio test: $\chi^2 = 1.85$, df =2, P = 0.397). Neither of the two test predictors (*i.e.*, FAIe and WAI) had an impact on habitat use (Table 4.3). However, habitat use was highly seasonal (Table 4.3, Figure 4.4)

Table 4.3 GLMM testing the effect of monthly food availability index (FAIe), monthly water availability index (WAI) on individual use of open habitat.

Term	Coded level	Estimate ± SE	χ2	P
(Intercept)		– 0.371 ± 0.328	–	–
Test predictors				
Food availability index (FAIe)[a]		0.100 ± 0.099	1.023	0.312
Water availability index[a]		– 0.161 ± 0.206	0.609	0.435
Control predictors				
Temporal autocorrelation term		**4.474 ± 0.192**	**229.990**	**< 0.001**
Cosine (Julian date)		**0.515 ± 0.181**	**24.052**[b]	**< 0.001**[b]
Sine (Julian date)		**1.411 ± 0.295**		
Sex[c]	Male	0.639 ± 0.376	2.543	0.111
Rainfall[a]		0.067 ± 0.056	1.638	0.201
Time of the day[a]		**0.356 ± 0.065**	**31.253**	**< 0.001**

n= 3554 scans. Statistically significant results ($p \leq 0.05$) appear in bold.
Focal ID (*n*=8) was included as random factor.
[a] square rooted transformed and then Z-transformed to a mean of 0 and a standard deviation of 1. Original means ± SD of the original variable: FAIe: 311629 ± 401087; WAI: 0.7 ± 0.2; rainfall: 0.03 ± 0.38; time of the day: 12.1 ± 3.0.
[b] Indicated is the overall test of the significance of season as obtained from comparing the full model with a reduced model lacking the two terms representing season.
[c] Estimate refers to the comparison with the reference categories: Sex: Female

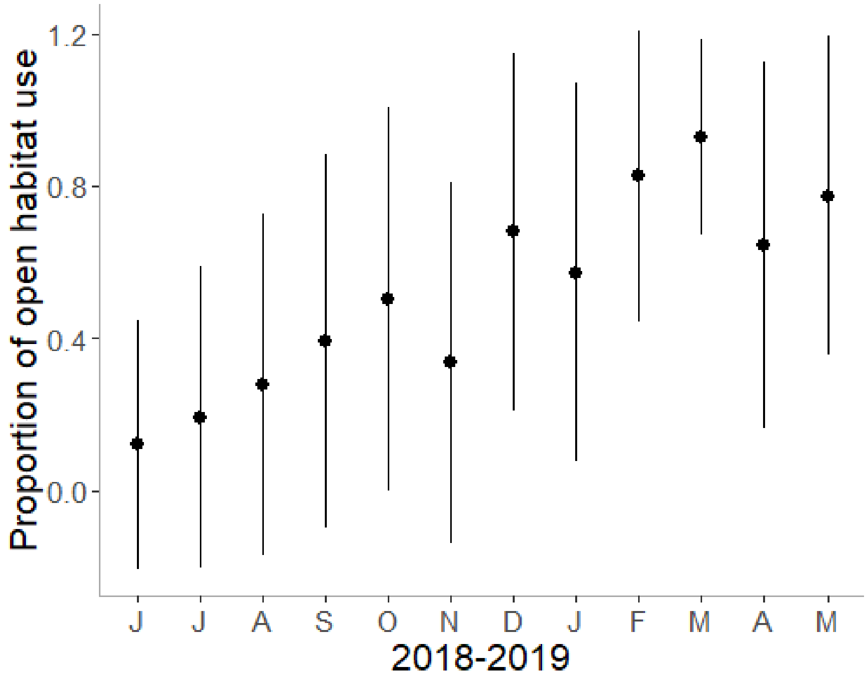


Figure 4.4 Issa chimpanzee monthly proportion of open habitat use (opposed to closed habitat) during the study period (June 2018-May 2019)

4. Discussion

Chimpanzee ranging patterns have been studied in several communities, mainly at forest sites, where annual HR generally falls between 6 and 37 km^2 (Table 4.1) and chimpanzees decrease their DPL in periods of low food availability. However, little is known about ranging patterns in open and dry savanna-woodland environments that are characterized by greater spatiotemporal fluctuations in resource availability. Investigating chimpanzee ranging in an understudied biome can yield important insights into chimpanzee adaptations and by analogy into early hominins adaptations to similar habitats. Using direct behavioral data from the Issa community, the present study provides data on 12 months of chimpanzee ranging patterns in a savanna-woodland, and especially in response to water as well as food availablity. Using two methods, MCP and GC, I estimated Issa community HR size, compared these results to other communities, and looked at monthly variations in HR. Running two different models, I tested whether fluctuations in DPL and habitat use were related to temporal variations in food and water availability at Issa.

4.1. Issa home range

The Issa chimpanzee HR was slightly larger than most other communities for which data are available (Table 4.1). Within-species variation in primate HR tends to be explained mainly by group/community size and food availability (Clutton-Brock and Harvey, 1977). Large groups generally have larger HR than smaller groups (Isbell, 1991; Janson and Goldsmith, 1995; Ganas and Robbins, 2005) and habitats in which food is scarce often result in larger HR than richer habitats (Takasaki, 1984; Campos *et al.*, 2014). At the time of the present study, the Issa community was comprised of 26 individuals, which is small compare to most communities (Vieira *et al.*, 2019), and thus unlikely explains the large HR observed at this site. However, the Issa landscape is characterized by a savanna-mosaic habitat known to have lower tree density than habitats with continuous forest cover (Crowther *et al.*, 2015), which may require chimpanzees to cover a larger area to find enough food to maintain dietary requirements. Nevertheless, the Issa range is much smaller than estimations based on indirect methods at savanna-woodland sites (*e.g.,* Baldwin *et al*, 1982; Suzuki, 1969; Kano, 1971). Issa HR is also smaller than figures reported for the Fongoli community (63–90 km^2: Pruetz, 2006; Pruetz and Herzog, 2017). Differences in HR sizes between Fongoli and Issa may also result from differences in habitat productivity/quality and food availability between the two sites. Annual precipitation has often been used as a proxy for primary productivity, with higher rainfall leading to higher productivity across habitats (van Schaik and Pfannes, 2005). Precipitation at Issa averages 1220 mm per annum (Piel *et al.*, 2017) compared to approx. 800 mm at Fongoli (Pruetz and Bertolani, 2009). These differences may result in potential higher productivity at Issa resulting in the smaller HR size observed. However, it is worth noting that habituation at Issa is recent and that the present study is the first attempt to calculate HR from direct follows. In the future we may observe an increase in chimpanzee HR estimate as Issa field team spend more time with the community and new areas in which chimpanzees range are recorded (as it has been the case at Fongoli; Pruetz, 2006).

I observed monthly variations in HR use with Issa chimpanzees shifting location throughout the year (Figure 4.2). These monthly shifts have been observed in other communities as well (Nyungwe: Moore *et al.*, 2018; M-group, Mahale: Turner, 2006). Uneven temporal and spatial distribution of resources could explain these variations. Although water availability may restrict ranging in some water-scarce landscapes (Moore, 1996), it is unlikely to explain temporal shifts in HR at Issa as water was available during the whole study period at different locations distributed accross Issa HR. Nonetheless, subsequent studies could examine temporal variations in water availability more precisely and at a finer scale across the various valleys of Issa range and investigate possible correlations with temporal variations in HR. However, food availability is more likely to explain the present study's results. From September to December 2018, chimpanzees shifted their usage to the southern areas of their territory (Figure 4.2). During these months they regularly fed on *Parinari curatellifolia* and *Garcinia huillensis* fruits (see Chapter 3), which may be more available in those areas. Similarly, Turner (2006) found that chimpanzees in the M-group at Mahale seasonally use lowland areas and grasslands in search of *Harungana madagascariensis* fruits and usually unexplored hilly areas to exploit temporary available

Salisia cerasifera fruits. The author concluded that the distribution of food resources could be the main factor explaining how chimpanzees use their HR. At Issa, future studies exploring botanical distribution coupled with phenology of important feeding species have the potential to shed light on the drivers of seasonal spatial shifts.

4.2. Daily path length model

In contrast to previous reports from other chimpanzee communities (Wrangham, 1977; Goodall, 1986; Matsumoto-Oda, 2002; Nakamura *et al.*, 2013; Green *et al.*, 2020), I found a negative correlation between DPL and food availability at Issa. This pattern could reflect an energy maximizing strategy, already described for baboons (Harding, 1976; Pebsworth *et al.*, 2012), gorillas (Ganas and Robbins, 2005) and lemurs (Overdorff, 1996) for instance. As such, Issa chimpanzees would increase the distance they travel each day to seek additional and/or valuable resources in order to maximize their nutrient intake rather than trying to minimize their energy expenditure during periods of food scarcity. However, when looking closely at monthly DPL patterns, I observed that during times where food availability was lowest (June–July and January–May), DPL did not necesseraly increase (Figure 4.3), questionning thus the probability of the energy maximizing strategy. Nevertheless, I observed an important reduction of mean DPL in November (Figure 4.3) when food avaibility was the highest at Issa. Monthly mean DPL was the highest in October and December but decreased in November (Figure 4.3). In November, although plant food was abundant chimpanzees spent much of their time feeding on *Macrotermes subhyalinus* termites (see Chapter 3). During termite season, Issa chimpanzees often remain several hours fishing on the same termite mound (pers. obs.). Termites are highly nutrituous and generally abundant in mound in November (see Chapter 3) but they are small feeding items that require a long processing time (make the tool, insert the tool in mound *etc.*) which encourage chimpanzees to stay at the same spot for prolonged periods. This might have resulted in a lower DPL during this particular month. A similar pattern, but linked to a different food item, has been described in North group at Taï, where chimpanzees decreased their DPL when large “superabundant” fig trees were in fruit (Doran, 1997). Although the model highlighted a positive correlation between DPL and food availability, DPL seems to be more influenced by specific characteristics of the feeding items seasonally available (*e.g.*, processing time, nutritional quality, patch abundance) than by the total food available in the HR. Where examination of phenology and feeding data on a more precise scale is possible, I recommend subsequent studies to investigate not only the importance of global fruit availability in influencing chimpanzee DPL, but also the productivity and nutritonial composition of individual important food species as well as the processing time/nutritional benefit ratio.

Contrary to my prediction, water availability did not influence Issa chimpanzee day range. Water availability impact on chimpanzee DPL has never been investigated before the present study; however, researchers have suggested that, in dry savanna-woodlands, chimpanzees would suffer from a persistent state of dehydration that could lead to behavioral responses (such as ranging adjustements) that would help to maintain water balance (Lindshield *et al.*, 2021). Other primates species, such as baboons and capuchins, reduced their travel distances and centred their activities around remaining water sources when water was restricted (Altmann and Altmann, 1970; Campos and Fedigan, 2009). Water acquisition has also been proposed to be an important factor involved in the survival and evolution of early human populations (Speth, 1987). The settlement of early hominins into open and dry savanna landscapes must have depended upon behavioral adaptations for locating and traveling between scattered water sources (Finlayson, 2013) and researchers have investigated extant primates behavioral responses to water scarcity to infer early hominins adaptations. Based on chimpanzee nesting patterns at Mt. Assirik (Senegal), Baldwin *et al.* (1982) hypothesized that their movements were constrained by having to access scarce, remaining water and that, by implication, by the end of the dry season, early hominin movements were likely restricted by the availability of temporary water courses. Alternatively, the data presented here suggest that chimpanzee ranging patterns at Issa are not determined by water availability and offer an alternative scenario in hominin behavior reconstructions. At Issa, during the study period, although water stopped flowing in some rivers during the latter part of the dry season, pools remained available in different areas of the HR, which might explain the lack of effect. Issa chimpanzees may possibly not suffer from dehydration, but it could also be possible that they employ other strategies than ranging to face periods of low water availability, such as diet adaptions with the consumptions of preformed water-rich foods (Wessling *et al.*, 2018), changes in activity budget to avoid activity during the hottest times of the day (Pruetz and Bertolani, 2009), or even physiological adaptations such as sweat glands modifications (Lindshield, 2014). Further investigations into potential physiological adaptations to water conservation, as well as examination of seasonal variation in activity budget and water content of important foods may help to clarify why Issa chimpanzee do not modify their ranging patterns during periods of low water availabilty as observed at other sites (Baldwin *et al.*, 1982). The findings of the present study highlight the variability of savanna-woodland sites and stress the need to improve chimpanzee sites' description along with the environmental variables that characterize them (van Leeuwen *et al.*, 2020) before considering that savanna-woodland sites necessarily impose greater challenges (such as dehydration) than forest sites (*e.g.,* Lindshield *et al.,* 2021).

Although I found a correlation between DPL and food availability, the model showed that seasonality had a greater effect on DPL. Seasonal variation in boundary patrols could be reflected by this seasonal term. At Ngogo for instance, chimpanzees increased the frequence of territorial boundary patrols before seasonal periods of food abundance, likely to evaluate the safety of the area (Mitani and Watts, 2005). At Mahale, individuals from M-Group ocasionally made incursions into the adjacent's K-group range, displacing the resident chimpanzees to feed on seasonally available foods (Nishida, 1979). Seasonal variations in the frequency of intergroup encounters and/or in the need to defend food from neighboring communities in peripheral areas may force Issa chimpanzees to increase their DPL at certain times of year. During the current study there were no inter-group encounters observed, and as of June 2021, only a single observation has been made (Drummond-Clarke, pers. obs). Future investigation into the correlation between DPL and inter-group encounters or boundary patrols rate at Issa may elucidate the seasonal variations in DPL at this site.

4.3. Habitat model

I found that neither food availability nor water availability impacted habitat use. Contrary to my prediction, Issa chimpanzees did not spend more time in open habitats during the low FAIe period. Open habitat use was the highest in December, February, March and May. Detailed analysis of Issa chimpanzee diet, especially during these months coupled with an analysis of the spatial distribution of important foods will inform on how temporal variations in Issa chimpanzees diet may influence habitat use. Also, water scarcity did not impact habitat use; Issa chimpanzees did not use evergreen forests more often when water was scarce. This confirms Hernandez-Aguilar (2009) observation on nests distribution at Issa during the dry season: nest site selection was not based on closeness to water. As for the DPL analysis, water may have been abundant enough at Issa to not impact habitat use and/or Issa chimpanzees may have used other behavioral or physiological strategies to cope with potential dehydration.

A likely key predictor of habitat use at Issa is predation, which I was not able to capture in the present study. Predation is a critical selective force that induces many behavioral adaptations among primates (Anderson, 1986). Specifically, the way in which primates use their habitat is influenced by both predation pressure and the perceived risk of predation in a given habitat (Hill and Dunbar, 1998). However, these variables likely exhibit seasonal fluctuations for a myriad of reasons. For instance, predators temporarily shift prey type (Goodman *et al.*, 1993) or HR (Wright *et al.*, 1997). The perception of predation risk by prey may vary spatially and temporally as well, peaking in locations and times where predators experience increased hunting success (Willems and Hill, 2009). The landscape of fear hypothesis proposes that prey recognize landscape-level heterogeneities in risk and respond by a number of anti-predator behaviors, including altering their habitat use to avoid risky areas (Coleman and Hill, 2014). For instance, vervet monkeys avoid dense thickets in which leopards can hide (Willems and Hill, 2009). Open woodlands constitute the majority of the chimpanzee savanna-woodland sites and are characterized by an open canopy and a grassy understory with sparse to dense grasses up to 1.8 meter high (Hernandez-Aguilar, 2009; van Leeuwen, 2019). Periodically, natural or human-induced fires occur in savanna-woodland landscapes and burn almost all ground cover in the woodland areas (Higgins *et al.*, 2007). Enhanced visibility associated with the burnt grass understory has been proven to lower temporally the individual perceived risk of predation among other primate species living in these kinds of landscapes and thus influence their habitat use (Rasmussen, 1983; Jaffe and Isbell, 2009). At Issa, during the study period, the first annual fires occurred by the end of July 2018 and the grass only started to grow back in October 2018 with the beginning of the rainy season (pers. obs.). Although the frequency of open habitat use was particularly low in July, it kept increasing until end of October (Figure 4.4) possibly as a consequence of the enhanced visibility in the burned open habitat. These results provide support for future fine scale analyses into the spatiotemporal distribution of predation risk and predation pressure at Issa and its relationship with habitat use. Predator density could be assessed from camera trap footage (Gerber *et al.*, 2010) whilst vigilance level and travel speed could be used as indirect metrics of risk perception in burned *versus* non burned areas (Laundré *et al.*, 2010), and thus shed light on temporal variation in chimpanzees habitat use at this site.

5. References

Alberts, S.C., Altmann, J., Hollister-smith, J.A., Mututua, R.S., Sayialel, S.N., Muruthi, P.M., Warutere, J.K., 2005. Seasonality and long term change in a savannah environment. In: Brockman, D.K., van Schaik, C.P. (Eds.), Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates. Cambridge University Press, Cambridge, pp. 157–195.

Altmann, J., 1974. Observational study of behavior: sampling methods. Behaviour. 49, 227–267.

Altmann, S., Altmann, J., 1970. Baboon Ecology: African Field Research. University of Chicago Press, Chicago.

Altmann, S.A., 1998. Foraging for Survival. Chigaco University Press, Chicago.

Amsler, S.J., 2009. Ranging behavior and territoriality in chimpanzees at Ngogo, Kibale National Park, Uganda. University of Michigan.

Anderson, C.M., 1986. Predation and primate evolution. Primates. 27, 15–39.

Baldwin, P.J., McGrew, W.C., Tutin, C.E.G., 1982. Wide-ranging chimpanzees at Mt. Assirik, Senegal. International Journal of Primatology. 3, 367–385.

Barton, R.A., Whiten, A., Strum, S.C., Byrne, R.W., Simpson, A.J., 1992. Habitat use and resource availability in baboons. Animal Behaviour. 43, 831–844.

Basabose, A.K., 2005. Ranging patterns of chimpanzees in a montane forest of Kahuzi, Democratic Republic of Congo. International Journal of Primatology. 26, 33–54.

Bates, L.A., Byrne, R.W., 2009. Sex differences in the movement patterns of free-ranging chimpanzees (*Pan troglodytes schweinfurthii*): foraging and border checking. Behavioral Ecology and Sociobiology. 64, 247–255.

Bertolani, M.P., 2013. Ranging and travelling patterns of wild chimpanzees at Kibale, Uganda: a GIS approach. University of Cambridge.

Boesch, C., Boesch-Achermann, H., 2000. The Chimpanzees of the Taï Forest: Behavioural Ecology and Evolution. Oxford University Press., Oxford.

Bromage, T.G., Schrenk, F., 1995. Biogreographic and climatic basis for a narrative of early hominin evolution. Journal of Human Evolution. 28, 109–114.

Campos, F.A., Bergstrom, M.L., Childers, A., Hogan, J.D., Jack, K.M., Melin, A.D., Mosdossy, K.N., Myers, M.S., Parr, N.A., Sargeant, E., Schoof, V.A.M., Fedigan, L.M., 2014. Drivers of home range characteristics across spatiotemporal scales in a Neotropical primate, *Cebus capucinus*. Animal Behaviour. 91, 93–109.

Campos, F.A., Fedigan, L.M., 2009. Behavioral adaptations to heat stress and water scarcity in white-faced capuchins (*Cebus capucinus*) in Santa Rosa National Park, Costa Rica. American Journal of Physical Anthropology. 138, 101–111.

Canale, C.I., Perret, M., Théry, M., Henry, P.Y., 2011. Physiological flexibility and acclimation to food shortage in a heterothermic primate. Journal of Experimental Biology. 214, 551–560.

Cerling, T.E., Wynn, J.G., Andanje, S.A., Bird, M.I., Korir, D.K., Levin, N.E., Mace, W., Macharia, A.N., Quade, J., Remien, C.H., 2011. Woody cover and hominin environments in the past 6 million years. Nature. 476, 51–56.

Chapman, C.A., Rothman, J.M., Lambert, J.E., 2012. Food as a selective force in primates. In: Mitani, J.C., Call, J., Kappeler, P.M., Palombit, R.A., Silk, J.B. (Eds.), The Evolution of Primate Societies. University of Chicago Press, Chicago, pp. 149–168.

Chapman, C.A., Wrangham, R.W., 1993. Range use of the forest chimpanzees of Kibale: Implications for the understanding of chimpanzee social organization. American Journal of Primatology. 31, 263–273.

Chapman, C.A., Wrangham, R.W., Chapman, L.J., 1995. Ecological constraints on group size : an analysis of spider monkey and chimpanzee. Behavioral Ecology and Sociobiology. 36, 59–70.

Charnov, E.L., 1976. Optimal foraging: the marginal value theorem. Theoretical Population Biology. 9, 129–136.

Cheng, Z., Ventura, M., She, X., Khaitovich, P., Graves, T., Osoegawa, K., Church, D., DeJong, P., Wilson, R.K., Pääbo, S., Rocchi, M., Eichler, E.E., 2005. A genome-wide comparison of recent chimpanzee and human segmental duplications. Nature. 437, 88–93.

Clutton-Brock, T.H., Harvey, P.H., 1977. Species differences in feeding and ranging behaviour in primates. In: Clutton-Brock, T.H. (Ed.), Primate Ecology: Studies of Feeding and Ranging Behavior in Lemurs, Monkeys, and Apes. Academic Press, London, pp. 557–584.

Coleman, B.T., Hill, R.A., 2014. Living in a landscape of fear: The impact of predation, resource availability and habitat structure on primate range use. Animal Behaviour. 88, 165–173.

Crowther, T.W., Glick, H., Covey, K., Bettigole, C., Maynard, D., Thomas, S., Al., E., 2015. Mapping tree density at a global scale. Nature. 525, 201–205.

Defler, T.R., 1996. Aspects of the ranging pattern in a group of wild woolly monkeys (*Lagothrix lagotricha*). American Journal of Primatology. 38, 289–302.

Dobson, A.J., 2002. An introduction to generalized linear model. Chapman & Hall/CRC, Boca Raton.

Doran, D., 1997. Influence of seasonality on activity patterns, feeding behavior, ranging, and grouping patterns in Taï chimpanzees. International Journal of Primatology. 18, 183–206.

Duvall, C.S., 2011. Biocomplexity from the ground Up: Vegetation patterns in a West African savanna landscape. Annals of the Association of American Geographers. 101, 497–522.

Fan, P.F., Jiang, X.L., 2008. Effects of food and topography on ranging behavior of black crested gibbon (*Nomascus concolor jingdongensis*) in Wuliang Mountain, Yunnan, China. American Journal of Primatology. 70, 871–878.

Fawcett, K.A., 2000. Female relationships and food availability in a forest community of chimpanzees . University of Edinburgh.

Finlayson, C., 2013. The water optimisation hypothesis and the human occupation of the mid-latitude belt in the Pleistocene. Quaternary International. 300, 22–31.

Foley, R.A., 1993. The influence of seasonality on hominid evolution. In: Ulijaszek, S.J., Strickland, S.S. (Eds.), Seasonality and Human Ecology: 35th Symposium Volume of the Society for the Study of Human Biology. Cambridge University Press, Cambridge, pp. 17–37.

Fox, J., Weisberg, S., 2011. An R Companion to Applied Regression, 2nd Edition. Thousand Oaks, CA: Sage.

Furtbauer, I., Mundry, R., Heistermann, M., Schu, O., Ostner, J., Fu, I., 2011. You mate , I mate : Macaque females synchronize sex not cycles. PLoS ONE. 6, 6–11.

Ganas, J., Robbins, M.M., 2005. Ranging behavior of the mountain gorillas (*Gorilla beringei beringei*) in Bwindi Impenetrable National Park, Uganda: A test of the ecological constraints model. Behavioral Ecology and Sociobiology. 58, 277–288.

Gerber, B., Karpanty, S.M., Crawford, C., Kotschwar, M., Randrianantenaina, J., 2010. An assessment of carnivore relative abundance and density in the eastern rainforests of Madagascar using remotely-triggered camera traps. Oryx. 44, 219–222.

Goodall, J., 1986. The chimpanzees of Gombe: Patterns of behavior. The Belknap Press of Harvard University Press, Cambridge.

Goodman, S.M., O'connor, S., Langrand, O., 1993. A review of predation on lemurs: implications for the evolution of social behavior in small, nocturnal primates. In: Kappeler, P.M., Ganzhorn, J.U. (Eds.), Lemur Social Systems and Their Ecological Basis. Plenum Press, New York, pp. 51–66.

Green, S.J., Boruff, B.J., Niyigaba, P., Ndikubwimana, I., Grueter, C.C., 2020. Chimpanzee ranging responses to fruit availability in a high-elevation environment. American Journal of Primatology. 82, 1–15.

Harding, R., 1976. Ranging patterns of a troop of baboons (*Papio anubis*) in Kenya. Folia Primatologica. 25, 143–185.

Hayne, D.W., 1949. Calculation of size of home range. Journal of Mammalogy. 30, 1–18.

Hemingway, C.A., Bynum, N., 2005. The influence of seasonality on primate diet and ranging. In: Brockman, D.K., van Schaik, C.P. (Eds.), Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates. Cambridge University Press, Cambridge, pp. 57–104.

Herbinger, I., Boesch, C., Rothe, H., 2001. Territory characteristics among three neighboring chimpanzee communities in the Taï National Park, Côte d'Ivoire. International Journal of Primatology. 22, 143–167.

Hernandez-Aguilar, R.A., 2009. Chimpanzee nest distribution and site reuse in a dry habitat : implications for early hominin ranging. Journal of Human Evolution. 57, 350–364.

Higgins, S.I., Bond, W.J., February, E., Bronn, A., Euston-Brown, D I W Enslin, B., Govender, N., Rademan, L., O'Regan, S., Potgieter, A.L.F., Scheiter, S., Sowry, R., Trollope, L., Trollope, W.S.W., 2007. Effects of four decades of fire manipulation on woody vegetation structure in Savanna. Ecology. 88, 1119–1125.

Hill, R.A., Dunbar, R.I.M., 1998. An evaluation of the roles of predation rate and predation risk as selective pressures on primate grouping. Behaviour. 135, 411–430.

Hunt, K.D., 1989. Positional behavior in Pan troglodytes at the Mahale Mountains and the Gombe Stream National Parks, Tanzania. University of Michigan.

Hunt, K.D., McGrew, W.C., 2002. Chimpanzees in the dry habitats of Assirik, Senegal and Semliki Wildlife Reserve, Uganda. In: Boesch, C., Hohmann, G., Marchant, L.F. (Eds.), Behavioural Diversity in Chimpanzees and Bonobos. Cambridge University Press, Cambridge, pp. 35–51.

Isbell, L.A., 1991. Contest and scramble competition: Patterns of female aggression and ranging behavior among primates. Behavioral Ecology. 2, 143–155.

Isbell, L.A., Young, T.P., 1996. The evolution of bipedalism in hominids and reduced group size in chimpanzees: alternative responses to decreasing resource availability. Journal of Human Evolution. 30, 389–397.

Itani, J., 1979. Distribution and adaptation of chimpanzees in an arid area. In: Hamburg, D.A., McCown, E.R. (Eds.), The Great Apes. Benjamin/Cummings, Menlo Park, pp. 52–72.

Izawa, K., 1970. Unit groups of chimpanzees and their nomadism in the savanna woodland. Primates. 11, 1–45.

Jaffe, K.E., Isbell, L.A., 2009. After the fire : Benefits of reduced ground cover for vervet monkeys (*Cercopithecus aethiops*). American Journal of Primatology. 71, 252–260.

Janson, C.H., Goldsmith, M.L., 1995. Predicting group size in primates : foraging costs and predation risks. Behavioral Ecology. 6, 326–336.

Jennrich, R.I., Turner, F.B., 1969. Measurement of non-circular home range. Journal of Theoretical

Biology. 22, 227–237.

Kalan, A.K., Kulik, L., Arandjelovic, M., Boesch, C., Haas, F., Dieguez, P., Barratt, C.D., Abwe, E.E., Agbor, A., Angedakin, S., Aubert, F., Ayimisin, E.A., Bailey, E., Bessone, M., Brazzola, G., Buh, V.E., Chancellor, R., Cohen, H., Coupland, C., Curran, B., Danquah, E., Deschner, T., Dowd, D., Eno-Nku, M., Michael Fay, J., Goedmakers, A., Granjon, A.C., Head, J., Hedwig, D., Hermans, V., Jeffery, K.J., Jones, S., Junker, J., Kadam, P., Kambi, M., Kienast, I., Kujirakwinja, D., Langergraber, K.E., Lapuente, J., Larson, B., Lee, K.C., Leinert, V., Llana, M., Marrocoli, S., Meier, A.C., Morgan, B., Morgan, D., Neil, E., Nicholl, S., Normand, E., Ormsby, L.J., Pacheco, L., Piel, A., Preece, J., Robbins, M.M., Rundus, A., Sanz, C., Sommer, V., Stewart, F., Tagg, N., Tennie, C., Vergnes, V., Welsh, A., Wessling, E.G., Willie, J., Wittig, R.M., Yuh, Y.G., Zuberbühler, K., Kühl, H.S., 2020. Environmental variability supports chimpanzee behavioural diversity. Nature Communications. 11, 1–10.

Kano, T., 1971. The chimpanzee of Filabanga, western Tanzania. Primates. 12, 229–246.

Koops, K., 2011. Chimpanzees in the Seringbara region of the Nimba Mountains. In: Matsuzawa, T., Humle, Y., Sugiyama, T. (Eds.), The Chimpanzees of Bossou and Nimba. Springer, Tokyo, pp. 277–287.

Laundré, J.W., Hernández, L., Ripple, W.J., 2010. The landscape of fear : Ecological implications of being afraid. The Open Ecology Journal. 3, 1–7.

Lehmann, J., Boesch, C., 2003. Social influences on ranging patterns among chimpanzees (*Pan troglodytes verus*) in the Taï National Park, Côte d’Ivoire. Behavioral Ecology. 14, 642–649.

Lehmann, J., Boesch, C., 2004. To fission or to fusion: Effect of community size on wild chimpanzee (*Pan troglodytes versus*) social organisation. Behavioral Ecology and Sociobiology. 56, 207–216.

Lehmann, J., Boesch, C., 2005. Bisexually bonded ranging in chimpanzees (*Pan troglodytes verus*). Behavioral Ecology and Sociobiology. 57, 525–535.

Lindshield, S., 2014. Multilevel analysis of the foraging decisions of western chimpanzees (*Pan troglodytes verus*) and resource scarcity in a savanna environment at Fongoli, Sénégal. Iowa State

University.

Lindshield, S., Hernandez-Aguilar, R.A., Korstjens, A.H., Marchant, L.F., Narat, V., Ndiaye, P.I., Ogawa, H., Piel, A.K., Pruetz, J.D., Stewart, F.A., van Leeuwen, K.L., Wessling, E.G., Yoshikawa, M., 2021. Chimpanzees (*Pan troglodytes*) in savanna landscapes. Evolutionary Anthropology

Matsumoto-Oda, A., 2002. Behavioral seasonality in Mahale chimpanzees. Primates. 43, 103–117.

McGrew, W.C., Baldwin, P.J., Tutin, C.E.G., 1981. Chimpanzees in a dry, hot and open habitat: Mt. Assirik, Senegal, West Africa. Journal of Human Evolution. 10, 227–244.

Milton, K., May, M.L., 1976. Body weight, diet and home range area in primates. Nature. 259, 459–462.

Mitani, J.C., Watts, D.P., 2005. Correlates of territorial boundary patrol behaviour in wild chimpanzees. Animal Behaviour. 70, 1079–1086.

Mitani, J.C., Watts, D.P., Amsler, S.J., 2010. Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. Current Biology. 20, 507–508.

Moore, J., 1992. Savanna Chimpanzees. In: Nishida, T., McGrew, W.C., Marler, P., Pickford, M., de Waal, F.B.M. (Eds.), Topics in Primatology, Vol. I: Human Origins. Tokyo Press University, Tokyo, pp. 99–118.

Moore, J., 1996. Savanna chimpanzees , referential models and the last common ancestor. In: McGrew, W.C., Marchant, L.F., Nishida, T. (Eds.), Great Ape Societies. Cambridge University Press, Cambridge, pp. 275–292.

Moore, J.F., Mulindahabi, F., Gatorano, G., Niyigaba, P., Ndikubwimana, I., Cipolletta, C., Masozera, M.K., 2018. Shifting through the forest: home range, movement patterns, and diet of the eastern chimpanzee (*Pan troglodytes schweinfurthii*) in Nyungwe National Park, Rwanda. American Journal of Primatology. 80, 1–13.

Muller, M.N., Wrangham, R.W., Pilbeam, D., 2017. Chimpanzees and human evolution. Harvard University Press, Cambridge.

N’guessan, A.K., Ortmann, S., Boesch, C., 2009. Daily energy balance and protein gain among pan troglodytes verus in the taï national park, côte d’Ivoire. International Journal of Primatology. 30,

481–496.

Nakamura, M., Corp, N., Fujimoto, M., Fujita, S., Hanamura, S., Hayaki, H., Hosaka, K., Huffman, M.A., Inaba, A., Inoue, E., Itoh, N., Kutsukake, N., Kiyono-Fuse, M., Kooriyama, T., Marchant, L.F., Matsumoto-Oda, A., Matsusaka, T., McGrew, W.C., Mitani, J.C., Nishie, H., Norikoshi, K., Sakamaki, T., Shimada, M., Turner, L.A., Wakibara, J. V., Zamma, K., 2013. Ranging behavior of Mahale chimpanzees: A 16 year study. Primates. 54, 171–182.

Newton-Fisher, N.E., 2003. The home range of the Sonso community of chimpanzees from the Budongo Forest , Uganda. African Journal of Ecology. 41, 150–156.

Nishida, T., 1979. The social structure of chimpanzees of the Mahale Mountains. In: McCown, E.R. (Ed.), The Great Apes. The Benjamin/Cummings Publishing Company, Menlo Park, pp. 73–121.

Nishida, T., Hiraiwa-Hasegawa, M., 1987. Chimpanzee and bonobos. In: Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W., Struhasker, T.T. (Eds.), Primate Societies. University of Chicago Press, Chicago, pp. 165–177.

Noser, R., Byrne, R.W., 2014. Change point analysis of travel routes reveals novel insights into foraging strategies and cognitive maps of wild baboons. American Journal of Primatology. 76, 399–409.

Ogawa, H., Idani, G., Moore, J., Pintea, L., Hernandez-Aguilar, A., 2007. Sleeping parties and nest distribution of chimpanzees in the savanna woodland, Ugalla, Tanzania. International Journal of Primatology. 28, 1397–1412.

Overdorff, D.J., 1996. Ecological correlates to activity and habitat use of two prosimian primates : Eulemur rubriventer and Eulemur fulvus rufus in Madagascar. American Journal of Primatology. 40, 327–342.

Passey, B.H., Levin, N.E., Cerling, T.E., Brown, F.H., Eiler, J.M., 2010. High-temperature environments of human evolution in East Africa based on bond ordering in paleosol carbonates. Proceedings of the National Academy of Sciences. 107, 11245–11249.

Pebsworth, P.A., Macintosh, A.J.J., Morgan, H.R., Huffman, M.A., 2012. Factors influencing the ranging behavior of chacma baboons (*Papio hamadryas ursinus*) living in a human-modified habitat.

International Journal of Primatology. 33, 872–887.

Piel, A.K., Strampelli, P., Greathead, E., Hernandez-Aguilar, R.A., Moore, J., Stewart, F.A., 2017. The diet of open-habitat chimpanzees (*Pan troglodytes schweinfurthii*) at Issa, Ugalla, western Tanzania. Journal of Human Evolution. 112, 57–69.

Pontzer, H., Wrangham, R.W., 2004. Climbing and the daily energy cost of locomotion in wild chimpanzees: Implications for hominoid locomotor evolution. Journal of Human Evolution. 46, 315–333.

Potts, R., 1998. Environmental hypotheses of hominin evolution. American Journal of Physical Anthropology. 107, 93–136.

Potts, R., 2013. Hominin evolution in settings of strong environmental variability. Quaternary Science Reviews. 73, 1–13.

Poulson, J.R., Clark, C.J., Smith, T.B., 2001. Seasonal variation in the feeding ecology of the grey-cheeked mangabey (*Lophocebus albigena*) in Cameroon. American Journal of Primatology. 54, 91–105.

Pruetz, J.D., 2006. Feeding ecology of savanna chimpanzees. In: Hohmann, G., Robbins, M.M., Boesch, C. (Eds.), Feeding Ecology in Apes and Other Primates. Cambridge University Press, Cambridge, pp. 161–182.

Pruetz, J.D., Bertolani, P., 2009. Chimpanzee *(Pan troglodytes verus*) behavioral responses to stresses associated with living in a savannah-mosaic environment: Implications for hominin adaptations to open habitats. PaleoAnthropology. 2009, 252–262.

Pruetz, J.D., Herzog, N.M., 2017. Savanna Chimpanzees at Fongoli, Senegal, Navigate a Fire Landscape. Current Anthropology. 58, 337–349.

Rasmussen, D.R., 1983. Correlates of patterns of range use of a troop of yellow baboons (*Papio cynocephalus*). II. Spatial structure, cover density, food gathering, and individual behaviour patterns. Animal Behaviour. 31, 834–856.

Scholz, F., Kappeler, P.M., 2004. Effects of seasonal water scarcity on the ranging behavior of Eulemur fulvus rufus. International Journal of Primatology. 25, 599–613.

Skinner, M.F., Pruetz, J.D., 2012. Reconstruction of periodicity of repetitive linear enamel hypoplasia from perikymata counts on imbricational enamel among dry-adapted chimpanzees (*Pan troglodytes verus*) from Fongoli, Senegal. American Journal of Physical Anthropology. 149, 468–482.

Speth, J.D., 1987. Early hominid subsistence strategies in seasonal habitats. Journal of Archaeological Science. 14, 13–29.

Stephens, D.W., Krebs, J.R., 1986. Foraging Theory. Princeton University Press, Princeton.

Stevenson, P.R., Quinones, M.J., Ahumada, J.A., 1994. Ecological strategies of woolly monkeys (*Lagothrix lagotricha*) at Tinigua National Park, Colombia. Journal of Primatology. 32, 123–40.

Stolwijk, A.M., Straatman, H., Zielhuis, G.A., 1999. Studying seasonality by using sine and cosine functions in regression analysis. Journal of Epidemiology and Community Health. 53, 235–238.

Strier, K.B., 2009. Seeing the Forest through the Seeds. Current Anthropology. 50, 213–229.

Suzuki, A., 1969. An ecological study of chimpanzees in a savanna woodland. Primates. 10, 103–148.

Takasaki, H., 1984. A model for relating troop size and home range area in a primate species. Primates. 25, 22–27.

Turner, L.A., 2006. Vegetation and chimpanzee ranging in the Mahale Mountains National Park, Tanzania. Memoirs of the Faculty of Science, Kyoto University. 18, 45–82.

van Leeuwen, K.L., 2019. Landscapes of the apes : Modelling landscape use of chimpanzees and early hominins across an environmental gradient. Bournemouth University.

van Leeuwen, K.L., Hill, R.A., Korstjens, A.H., 2020. Classifying chimpanzee (*Pan troglodytes*) landscapes across large-scale environmental gradients in Africa. International Journal of Primatology. 41, 800–821.

Van Schaik, C.P., Terborgh, J.W., Wright, S.J., 1993. The phenology of tropical forests: Adaptive significance and consequences for primary consumers. Annual Review o f Ecology and Systematics. 24, 353–377.

van Schaik, Carel P, Pfannes, K.R., 2005. Tropical climates and phenology : a primate perspective. In:

Brockman, D.K., van Schaik, C P (Eds.), Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates. Cambridge University Press, Cambridge, pp. 23–54.

Vieira, W.F., Kerry, C., Hockings, K.J., 2019. A comparison of methods to determine chimpanzee home-range size in a forest-farm mosaic at Madina in Cantanhez National Park, Guinea-Bissau. Primates. 60, 355–365.

Vogel, E.R., Knott, C.D., Crowley, B.E., Blakely, M.D., Larsen, M.D. and Dominy, N.J., 2012. Bornean orangutans on the brink of protein bankruptcy. Biology Letters. 8, 8333–8336.

Watts, D.P., Potts, K.B., Lwanga, J.S., Mitani, J.C., 2012. Diet of chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo, Kibale National Park, Uganda, 2. Temporal variation and fallback foods. American Journal of Primatology. 74, 130–144.

Wessling, E.G., Kühl, H.S., Mundry, R., Deschner, T., Pruetz, J.D., 2018. The costs of living at the edge : Seasonal stress in wild savanna-dwelling chimpanzees. Journal of Human Evolution. 121, 1–11.

White, T.D., Asfaw, B., Beyene, Y., Haile-Selassie, Y., Lovejoy, C.O., Suwa, G., WoldeGabriel, G., 2009. Ardipithecus ramidus and the paleobiology of early hominids. Science. 326, 64–86.

Willems, E.P., Hill, R.A., 2009. Predator-specific landscapes of fear and resource distribution : Effects on spatial range use. Ecology. 90, 546–555.

Williams, J.M., Pusey, A.E., Carlis, J. V., Farm, B.P., Goodall, J., 2002. Female competition and male territorial behaviour influence female chimpanzees’ ranging patterns. Animal Behaviour. 63, 347–360.

Wilson, M.L., 2001. Imbalances of power: How chimpanzees respond to the threat of intergroup aggression. Harvard University.

Worman, C.O., Chapman, C.A., 2005. Seasonal variation in the quality of a tropical ripe fruit and the response of three frugivores. Journal of Tropical Ecology. 21, 689–697.

Wrangham, R.W., 1977. Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In: Clutton-Brock, T. (Ed.), Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes. Academic Press, London, pp. 503–538.

Wrangham, R.W., 1979. Sex differences in chimpanzee dispersion. In: Hamburg, D.A., McCown, E.R. (Eds.), The Great Apes. Benjamin/Cummings, Menlo Park, pp. 481–489.

Wrangham, R.W., 1980. An ecological model of female-bonded primate groups. Behaviour. 75, 262–300.

Wright, P.C., Heckscher, K.S., Dunham, A.E., 1997. Predation on Milne-Edward's sifaka (*Propithecus diadema edwardsi*) by the Fossa (*Cryptoprocta ferox*) in the rain forest of Southeastern Madagascar. Folia Primatologica. 68, 34–43.

6. Appendix

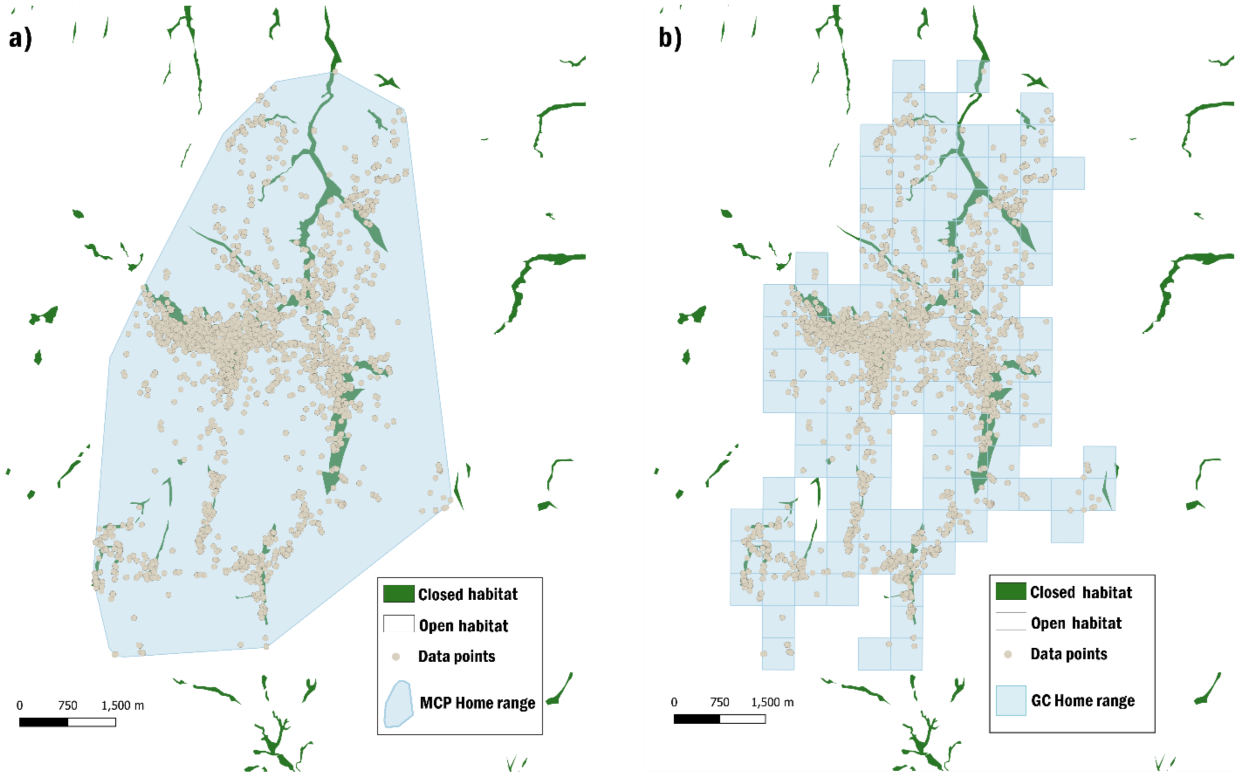


Figure 4.A.5 Home range estimates using two different methods: **a)** maximum convex polygon (MCP) which involves creating a polygon with convex angles around all data points **b)** grid cell (GC) which consists of superimposing a 500 × 500 m cells grid over the study area and selecting only the cells with data points.

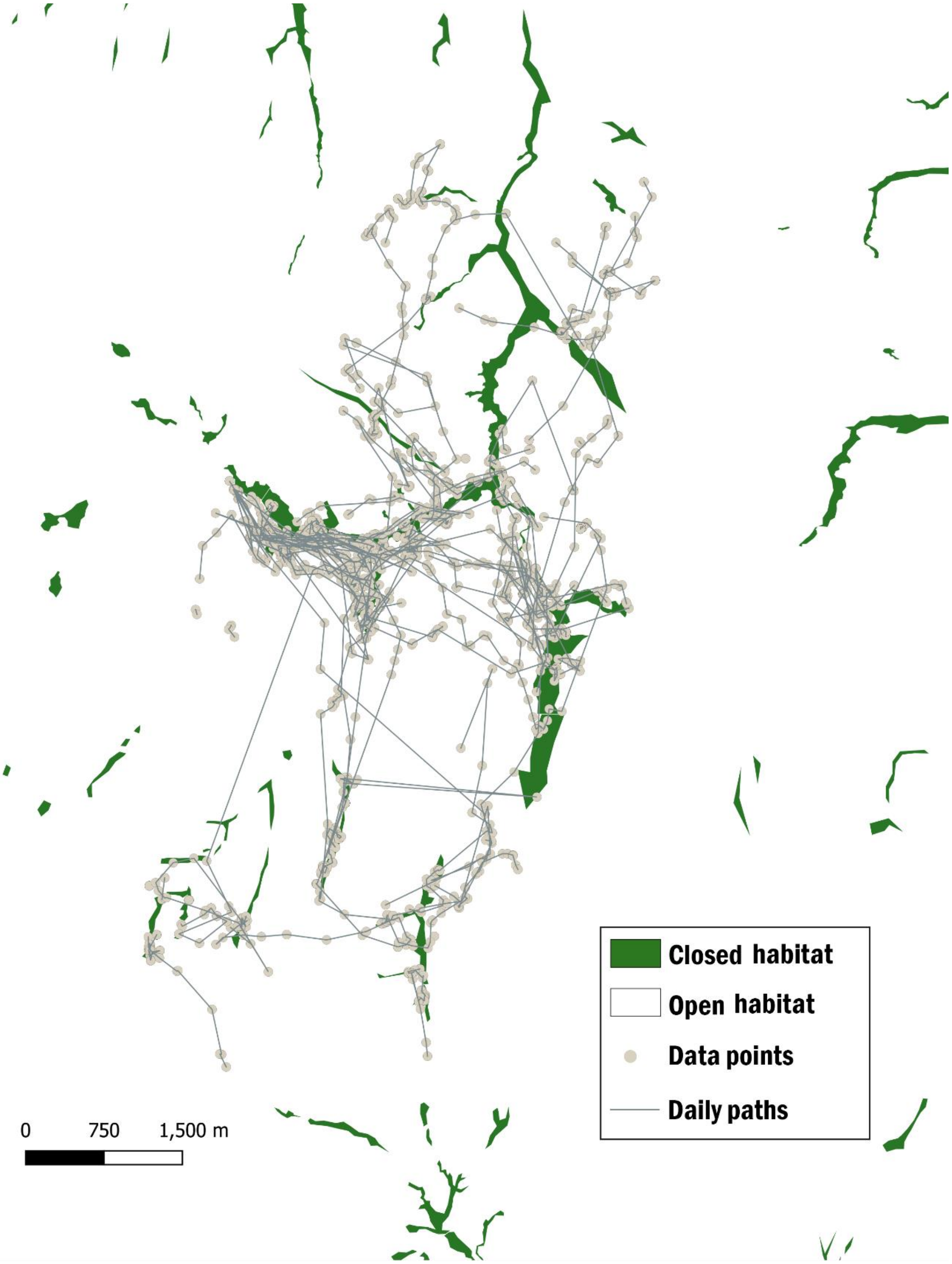


Figure 4.A.6 Imba's (one of the male chimpanzees at Issa) daily paths during the study period created by joining consecutive way-points for a given day with a straight-line segment.

Chapter 5: Chimpanzee grouping patterns in the open, dry and seasonal savanna-woodland of Issa

Submitted for a publication in the Journal of Human Evolution (accepted with minor revisions) and reformatted to fit the thesis requirements.

1. Introduction

The term fission-fusion was first introduced to describe social systems where group size varies by the splitting (fission) or merging (fusion) of subgroups (Kummer, 1971). While many group-living mammals occasionally split into smaller units, some species such as bottlenose dolphins (*Tursiops truncatus*: Connor *et al.*, 2000), spotted hyenas (*Crocuta crocuta*: Holekamp *et al.*, 1997), African elephants (*Loxodonta africana*: Wittemyer *et al.*, 2005), spider monkeys (*Ateles* spp.: Klein and Klein, 1971), chimpanzees (*Pan troglodytes*: Nishida, 1968) and bonobos (*P. paniscus:* Kano, 1982) do this on a regular basis, with subgroup size and composition fluctuating by day or even hour (Aureli *et al.*, 2008). This social organization is thought to have evolved as an adaptation that balances costs (*e.g.*, food competition) and benefits (*e.g.*, reduced predation risk) of group living in a fluid way as resources and constraints shift over space and time (Bertram, 1978; Terborgh and Janson, 1986; Dunbar, 1988; Sueur *et al.*, 2011).

Chimpanzees, which rely mainly on ripe fruit, a resource characterized by its spatiotemporal fluctuations in distribution, might struggle to maintain viable communities if they did not temporarily fission into small subgroups (Lehmann *et al.*, 2007a). Although individual chimpanzees belong to a community in which all members associate, they split into smaller groups (or parties) while the entire community rarely aggregates (Sugiyama, 1968). Examining factors that regulate chimpanzee party size is important because it informs on what constraints a community might be facing (*e.g.*, resource fluctuations) and how individuals socially respond to them (Terborgh and Janson, 1986; Schulke and Ostner, 2012). Two measures of chimpanzee party size are frequently discussed in the literature (Table 5.1): (1) absolute party size (APS), which is the number of individuals in a party and (2) relative party size (RPS), which is the percentage of the community that composes the party (APS/community size × 100; Boesch, 1996) and is often used as a proxy for community cohesion (Furuichi, 2009). Researchers have varied in their operational definition of chimpanzee 'party' over the last half century (Table 5.1) and definitions impact party size calculations (Chapman *et al.*, 1993; Hashimoto *et al.*, 2001).

Table 5.1 Comparison of mean absolute party size (APS), mean relative party size (RPS) and methods used to calculate it in different studies based on direct observations.

Community	**Hab**	**Community size**		**APS**		**RPS**	**Method**	**Source**
		w/o dep.	with dep.	w/o dep.	with dep.			
Assirik	SW	~16	~24		5.3	—	All individuals present upon first contact	Tutin *et al.*, 1983
Assirik	SW	—	~28	4.0	—	—	All indep. present upon first contact	Hunt and Mc Grew, 2002
Bossou	F	13	20	4.0	—	30.8	All indep. encountered in a single day	Sakura, 1994
Bossou	F	9	14	5.0	—	55.6	All indep., 5-minute scan	Hockings *et al.*, 2012
Bossou	F	10	13	—	6.8	52.3	All individuals, 15-minute scan	Bryson-Morrison, 2017
Budongo (Sonso)	F	—	46	—	5.0	10.9	All individuals, 30-min scans	Newton-Fisher *et al.*, 2000
Budongo (Sonso)	F	31	43	—	5.6	13.0	All individuals traveling together	Wallis, 2002
Budongo (Sonso)	F	36	71	7.3	—	20.4	All indep., continuous	Villioth, 2018
Budongo (Waibira)	F	46	88	4.4	—	9.5	All indep., continuous	Villioth, 2018
Fongoli	SW	17	35	—	15.0	42.9	All individuals encountered in a single day	Pruetz and Bertolani, 2009
Gashaka-Gumti	F	—	35	—	4.1	11.7	All individuals (w/o infants) encountered	Sommer *et al.*, 2004
Gombe	F	28	43	—	11.9	27.7	All individuals traveling together	Wallis, 2002
Gombe	F		57	—	5.6	9.8	All individuals, continuous	Goodall, 1986
Issa	SW	18	26	5.6	—	30.3	All indep. seen in one hour	this study
Kahuzi-Biega	F	14	22		4.4	20.1	All individuals in foraging parties	Basabose, 2004
Kalinzu	F	45	—	5.9	—	13.0	All indep. seen in one hour	Hashimoto *et al.*, 2001
Kibale (Kanyawara)	F	27	—	5.1	—	18.8	All indep., 15-min scan	Chapman *et al.*, 1995
		—	—	5.1	—	18.9	All indep., continuous	
		—	—	7.1	—	26.4	All indep. seen in one hour	
Kibale (Kanyawara)	F	30	55	7.0	—	23.3	All indep., 15-minute scan	Pokempner, 2009
Kibale (Ngogo)	F	101	145	6.7	—	6.6	All indep., 30-min scan (parties with female)	Wakefield, 2008
Kibale (Ngogo)	F	95	140	10.3	—	10.8	All indep. present upon first contact	Mitani *et al.*, 2002
Mahale (M)	F	45	85	—	24.6	28.9	All individuals encountered in a single day	Matsumoto-Oda, 1998
Mahale (M)	F	31	44	4.0	—	12.1	All indep., 1-min scan	Itoh and Nishida, 2007
		—	—	15.5	—	47.0	All indep. encountered in a single day	
Semliki	SW	—	≥29	4.8	—	—	All indep. present upon first contact	Hunt and Mc Grew 2002
Taï (North)	F	—	76		8.0	10.5	All individuals, continuous	Boesch *et al.*, 1996
Taï (North)	F	36	70	3.5	—	9.6	All indep. seen in one hour	Doran *et al.*, 1997
Taï (North)	F	17	31	5.5	—	32.4	All indep., 15-minute scan	Anderson *et al.*, 2002
Taï (South)	F	25	39	5.2	—	20.8	All indep., continuous	Wittiger and Boesch, 2013

hab.: habitat, SW: savanna-woodland, F: forest, w/o: without, dep.: dependent individuals *i.e.*, infants and juveniles, indep.: independent individuals

For example, ‘nomadic’ APS (all individuals observed over the course of a day) provides a 40% larger estimate than APS calculated at 15-minute intervals (Chapman *et al.*, 1994). Methodological discrepancies are difficult to overcome given the specificities of each chimpanzee study site (vegetation, terrain, number of observers, degree of habituation, *etc.*), making inter-site comparisons difficult and limiting our ability to universally assess party-size determinants.

Despite methodological heterogeneity, variation in chimpanzee APS has been explained by temporal variation in food availability in several communities (Nishida, 1979; Chapman, 1990; Anderson *et al.*, 2002; Korstjens *et al.*, 2006; Lehmann *et al.*, 2007a), with individuals splitting into small parties when food is scarce as a way of reducing feeding competition and aggregating in larger parties during periods of food abundance. Other studies, in some cases based on data from these same communities, reported no effect of food availability on APS (Table 5.2). This inconsistency could result from a curvilinear relationship between food availability and APS (Newton-Fisher *et al.*, 2000). That is, as global food availability increases, the constraints of limited food supply weaken, until it has almost no influence on APS. At Ngogo (Kibale, Uganda) for example, where food productivity is considered to be high all year (Wakefield, 2008), (female) APS was not influenced by food availability (Wakefield, 2008), potentially because it did not reach low enough levels to limit party size (Hashimoto *et al.*, 2001). For this reason, seasonal periods of food scarcity (more than global food availability) may shape chimpanzee grouping behavior. Along with food, the availability of surface water for drinking likely has an impact on chimpanzee APS and overall daily activities (McGrew *et al.*, 1981). At sites where water is seasonally scarce, chimpanzees prefer to feed close to water (Lindshield *et al.*, 2017) and may aggregate in larger parties at the few water sources remaining during the dry season (Tutin *et al.*, 1983; Pruetz and Bertolani, 2009).

In addition to resource availability, the presence of sexually receptive females is consistently associated with greater APS across communities (Table 5.2). Female chimpanzees reproduce only every 5–6 years (Tutin and McGinnis, 1981; Nishida *et al.*, 1990; Boesch and Boesch-Achermann, 2000) and are thus a limiting source for males that aggregate around them during periods of sexual receptivity (Deschner *et al.*, 2003). Female chimpanzees are most sexually receptive when they exhibit a maximal anogenital swelling, which lasts for approximately 10–12 days (Goodall, 1986; Wallis, 1997), although they do attract males also when swellings are not at their maximal size (Tutin and McGinnis, 1981;

Hasegawa and Hiraiwa-Hasegawa, 1983). Joining parties with swollen females may also be advantageous for other females as the formers' presence may stimulate the resumption of postpartum cycles for mothers and initiate the first full anogenital swelling in nulliparous females (Wallis, 1992).

Table 5.2 Factors tested for their impact on absolute party size at various field sites.

Community	**Food availability**[a]	**Swollen females**	**Other**	**Source**
Assirik	Rainfall NS	Swollen females +	Activity (largest when traveling) Habitat (largest in open)	Tutin *et al.*, 1983
Bossou	—	Swollen females +	Presence of danger +	Sakura, 1994
Bossou	Fruit availability NS	Swollen females +	—	Hockings *et al.* 2012
Budongo (Sonso)	Food abundance NS	—	Patch size +	Newton-Fisher *et al.*, 2000
	Fruit abundance NS	—	—	
Budongo (Sonso)	—	Swollen females +	—	Wallis, 2002
Fongoli	Rainfall +	—	—	Pruetz and Bertolani, 2009
Gashaka-Gumti	Rainfall NS	Swollen females +	—	Sommer *et al.*, 2004
Gombe	—	Swollen females +	—	Wallis, 2002
Kahuzi-Biega	Fruit abundance NS	—	—	Basabose, 2004
	Fruit distribution +	—	—	
Kalinzu (M group)	Fruit abundance NS	Swollen females +	—	Hashimoto *et al.*, 2001
	Fruit distribution NS	—	—	
Kibale (Kanyawara)	Fruit abundance +	—	—	Chapman *et al.*, 1995
	Fruit distribution +	—	—	
Kibale (Ngogo)	Fruit availability NS	Swollen females +	—	Wakefield, 2008
Kibale (Ngogo)	Food availability +	Swollen females +	—	Mitani *et al.*, 2002
	Rainfall NS	—	—	
Mahale (M-Group)	Fruit abundance +	Swollen females +	—	Matsumoto-Oda, 1998
Mahale (M-Group)	Fruiting plant density +	—	Tree patch size +	Itoh and Nishida, 2007
Seringbara (Guinea)	Fruit availability +	Swollen females +	—	van Leeuwen *et al.*, 2020b
Taï (North)	Fruit availability +	—	Predation pressure -	Boesch, 1991
Taï (North)	Fruit availability +	Swollen females +	Activity NS	Boesch, 1996
	—	—	DBH +	
	—	—	Hunting rate +	
Taï (North)	Rainfall +	—	—	Doran *et al.*, 1997
Taï (North)	Fruit abundance NS	Swollen females +	Activity of focal animal (largest when meat eating)	Anderson *et al.*, 2002
	Fruit distribution NS	—	Day time (largest early morning and late afternoon)	
Taï (East and South)	Fruit availability NS	Swollen females +	Group defense score +	Samuni *et al.*, 2020
	—	—	Territorial activity +	

[a] Different estimations of food availability have been used depending on the study. I included the variable rainfall in this column as it is often used as a proxy for food availability. + positive correlation, NS: non-significant

Additionally, predation is an important force that has long been discussed to shape primate group size (Alexander, 1974; van Schaik and Hörstermann, 1994), and understanging how individuals manage the risk of predation is a central issue in the study of primate grouping patterns (Aureli *et al.*, 2008). The perception of predation risk by prey varies spatially, peaking in locations where predators experience increased hunting success (Willems and Hill, 2009). The landscape of fear hypothesis proposes that prey respond to spatially-heterogenous risk by adapting their anti-predatory behavior to the location in which they are (Coleman *et al.*, 2014). Increasing group size is an efficient anti-predator strategy because larger groups exhibit enhanced vigilance, benefit from the dilution effect, and offer better defense mechanisms in case of a predator attack (Dunbar, 1988). As an illustration of this phenomenon, white-bellied spider monkeys *(Ateles belzebuth)* increase APS when visiting mineral licks, probably because they face high predation risk in these areas (Link and Di Fiore, 2013). Unfortunately, the effect of predation on chimpanzee APS has been largely neglected (but see Boesch, 1991), likely due to the difficulty of observing predation events on chimpanzees. Despite their relatively large body mass, chimpanzees suffer predation from leopards (*Panthera pardus*: Boesch, 1991; Zuberbühler and Jenny, 2002; Henschel *et al.*, 2005; Nakazawa *et al.*, 2013) and lions (*Panthera leo*: Tsukahara, 1993; Nishida, 2012). Wild dogs (*Lycaon pictus*) and hyenas (*Crocuta crocuta*) are other potential predators (Stewart and Pruetz, 2013; McLester *et al.*, 2016). In one of the only attempts to examine the impact of predation on chimpanzee party size, Boesch (1991) found that Taï chimpanzees in the Ivory Coast surprisingly decreased APS in response to increased predation pressure (defined as the number of leopard encounters per month). The author suggested that, in the very dense Taï forest, large parties may be very noisy and easily detectable by leopards, making smaller parties one anti-predator strategy in this habitat.

Whilst predation from carnivores likely influences chimpanzee APS in ways that have not been systematically studied, humans, as well as neighboring chimpanzee communities, also affect grouping patterns. Similar to predator attacks, human confrontations (Boesch and Boesch-Achermann, 2000) as well as chimpanzee inter-group conflicts (Wilson *et al.*, 2014) may lead to severe injuries and/or death in chimpanzees. In general, carnivores, humans, and neighboring communities may all be perceived as danger for chimpanzees and may elicit similar grouping pattern responses. For instance, chimpanzees at Bossou (Guinea) and at Fongoli (Senegal) enter anthropogenic areas (such as roads and cultivated fields) in larger parties (Sakura, 1994; Hockings *et al.*, 2012; Lindshield *et al.*, 2017). In the case of inter-community encounters, larger parties are favorable, with most intercommunity killings occurring when attackers overwhelmingly outnumber their victims (Wilson *et al.*, 2014). As an illustration of this, Taï chimpanzees form larger parties during months when individuals participate in territorial activities (*i.e.*, border patrol and intergroup encounters, Samuni *et al.*, 2020) and at Kanyawara (Kibale, Uganda), APS was larger when parties were close to the home range edges as compared to core areas (Wilson, 2001).

Understanding how spatiotemporal fluctuations in various biotic and abiotic factors shape chimpanzee grouping patterns sheds light on what challenges a community might experience (intergroup encounters, predation, variation in resource availability, *etc.*), but also has bearing on reconstructions of hominin evolution (Grueter *et al.*, 2012). Given their close genetic relationship to humans (Cheng *et al.*, 2005) and morphological similarity to australopithecines (*e.g.*, Berger and Tobias, 1996), common chimpanzees are frequently used as referential models to understand human evolution (*e.g.*, Wrangham, 1987; Moore, 1996, DeSilva, 2009; Prang *et al.*, 2021 but see Sayers and Lovejoy, 2008). Various authors have argued that ancestral hominin species were most likely characterized by a chimpanzee-like fission-fusion society with large numbers of bonded males, and immigrant females (Wrangham, 1987; Chapais, 2010; van Schaik, 2016).

Whereas most studies of wild chimpanzees to date have focused on forest-dwelling populations (Lindshield *et al.*, 2021), extant chimpanzees live across a gradient of habitats from tropical rainforests to open and dry savannas (van Leeuwen *et al.*, 2020a). Investigation of the latter allows us to ask questions that are more ecologically relevant to Plio-Pleistocene hominin evolution, which largely occurred in similarly open and dry savanna-mosaic environments (Davies *et al.*, 2020). A major climatic shift occurred during the late Pliocene (~3.0−2.6 Ma) resulting in a concomitant transition from closed canopy forests toward more open and dry habitats (Robinson *et al.*, 2017). Specifically, reconstructions of post-climatic shifts in Plio-Pleistocene environments describe a combination of woodlands, bushlands, riparian forests, and seasonal flood plains that were characterized by high seasonality in rainfall (Reed and Fish, 2005; Cerling *et al.*, 2011), a landscape very similar to that of some extant chimpanzee communities, such as Issa (Tanzania). Constraints associated with a heterogenous, and seasonal environment were a major challenge faced by Plio-Pleistocene hominins (Foley, 1993; Cerling *et al.*, 2011) and it was partly their adaptation and response to such constraints that formed the basis for the divergence of the hominin lineage (Potts, 2013). Understanding the grouping strategies of one of our closest living relatives potentially facing similar environmental constraints as early hominins did, may help us better identify the patterns involved in human evolutionary adaptations to these environments.

Chimpanzee habitats have long been dichotomized as being either savanna or forest dwelling (reviewed in van Leeuwen *et al.*, 2020a). The former (also described as open and dry landscapes) have historically been classified as savannas despite often comprising a heterogenous mosaic of woodlands, grasslands, swamps, and closed-canopy evergreen forests (Bourliere and Hadley, 1983). These sites are regularly described as marginal for chimpanzees compared to more forested sites (Kortlandt, 1983; Moore, 1992; Pruetz and Bertolani, 2009, Lindshield et al., 2021) as they tend to receive less than 1360 mm of annual rainfall (van Leeuwen *et al.*, 2020a) and exhibit long dry seasons (defined as the number of consecutive months having less than 100 mm of rainfall, Hunt and McGrew, 2002) that result in dramatic seasonal fluctuations in food and water availability (*e.g.*, Pruetz, 2006). Forest-dwelling chimpanzees also face seasonality, but the magnitude of seasonal variation in climate and food availability is comparatively moderate (Wessling *et al.*, 2018a). Savanna-woodland sites also have lower forest cover (<12.5%, van Leeuwen *et al.*, 2020a) with lower tree diversity (Crowther *et al.*, 2015) and thus fewer chimpanzee-feeding trees (in number and species diversity) compared to forested environments (Isbell and Young, 1996; Potts and Lwanga, 2014; Wessling *et al.*, 2020). In a comparative study between Fongoli and Taï chimpanzees, Wessling *et al.* (2018a) found that total food availability was lower year-round at Fongoli, but ripe fruit availability was higher. Finally, predation pressure and risk are proposed to be higher in savanna sites because they host greater predator diversity, and fewer escape opportunities compared to forests (Tutin *et al.*, 1983).

Early studies of chimpanzees living in these landscapes hypothesized that they would show variation in their sociality compared to forest-dwelling communities as a response to the ‘extreme’ environment (Suzuki, 1969; Izawa, 1970; Kano, 1971; Kortlandt, 1983; Tutin *et al.*, 1983; Moore, 1996). They may be more cohesive (*i.e.*, larger RPS) than forest-dwelling communities as a way to cope with predation (Tutin *et al.*, 1983). The first (and only to date) results that described APS and RPS in a savanna community came from Fongoli, where Pruetz and Bertolani (2009) found that both APS and RPS were higher than what has been reported in other communities, which may be a savanna adaptation. In that study, the authors defined party as all individuals observed on a given day (*i.e.*, nomadic party size), which is demonstrated to overestimate APS compared to other methods (Chapman *et al.*, 1994). However, even after reducing their estimates by 40% (as suggested by Chapman *et al.*, 1994), RPS at Fongoli (26%) was still larger than most reported values from other communities (Table 5.1). Unfortunately, no thorough examination of factors (*e.g.*, fluctuations in food and water availability, predation risk, *etc.*) potentially influencing party size at this site was made, and only seasonal trends (dry *versus* wet season) were reported.

It may not just be habitat that influences RPS. Studies from the forest-dwelling communities of Taï and Bossou revealed that chimpanzees were also highly cohesive (Boesch, 1996; Anderson *et al.*, 2002; Hockings *et al.*, 2012; Wittiger and Boesch, 2013; Bryson-Morrison *et al.*, 2017), especially when compared to the East African chimpanzee (*P. t. schweinfurthii*) communities of Gombe and Mahale (Tanzania), as well as Budongo (Uganda). Rather than cohesion being a response to the local habitat, it was suggested that increased cohesion could be specific to the western subspecies (*P. t. verus*; Boesch, 1996) and that West African communities may be intermediate between the high degree of cohesion observed in bonobos (*P. paniscus*) and lower degree seen in East African chimpanzees (*e.g.*, Yamakoshi, 2004).

We lack data from additional savanna-woodland sites and especially from East African communities to disentangle the drivers of community cohesiveness and identify if a clear distinction between forest *versus* savanna-woodland and/or eastern *versus* western grouping patterns can be made (Lindshield *et al.*, 2021). Furthermore, investigation into chimpanzees that experience an open and dry landscape can shed light on how early hominins may have adapted to similar constraints. For instance, savanna-woodland sites are more likely to show great seasonal fluctuations in resources such as food and water availability that are likely to influence grouping patterns in ways that have not yet been explored.

Finally, if grouping patterns are a response to predation, we stand to gain most by asking these questions in places where predators have not been extirpated, as they have largely been in Fongoli (Stewart and Pruetz, 2013). To that end, in the current study I examined grouping patterns of a chimpanzee community living in the Issa Valley, located ~100 km east of the eastern shore of Lake Tanganyika, western Tanzania. The Issa landscape is a combination of heterogenous vegetation where forest represents only 7% of vegetation cover. The region receives lower annual rainfall than the majority of chimpanzee sites and is characterized by a prolonged dry season. I addressed the following questions:

(1) What are the factors shaping chimpanzee APS at Issa?

(2) How does cohesion (measured with RPS) in the Issa community compare to other chimpanzee communities?

I hypothesized that APS would be influenced by four key predictors: food availability, the presence of sexually receptive females, habitat structure and water availability. Considering the seasonality in rainfall and potential associated fluctuations in food availability at Issa, I expected that APS would be positively correlated with food availability. I also expected the presence of swollen females to play a significant role in explaining APS at Issa, similar to other communities. Given the presence of predators and the heterogeneity of the habitat at Issa, I expected chimpanzees to adjust their APS to perceived predation risk in the different habitats. I expected parties to be larger in open habitat as a strategy to confront potentially higher predation risk in areas that offer fewer escape routes than in closed habitat. I further expected water availability to have an impact on APS at Issa with larger parties observed during periods of low water availability due to individuals aggregating around water sources. Finally, I hypothesized that the potentially extreme environmental characteristics of the Issa landscape would influence community cohesion. I therefore expected that the Issa community will be highly cohesive (*i.e.*, high mean RPS) similar to what has been described at Fongoli, rather than expecting less cohesion at Issa due to previously hypothesized sub-species differences in sociality.

2. Material and methods

2.1. Data collection

Food availability

I calculated a food availability index based on the ten most important plant food items in the Issa chimpanzee diet (see Chapter 2 for details) using the following formula:

$$FAIe_m = \sum_{1}^{10} P_{ism} \times BA_{si} \times M_i \times E_i$$

where P_{im} denotes the mean abundance of item *i* on species *s* in month *m*, BA_{si} represents the basal area per hectare in Issa area for the species *s* to which the item *i* belongs, M_i represents the average dry mass for item *i* and E_i represents the average energy per gram of dry mass for item *i*.

Water availability

I calculated a water availability index (WAI) based on Wessling *et al.* (2018b) (see Chapter 2 for details) and used the following equation:

$$WAI_m = \sum_{1}^{8} \frac{Depth_{im}}{Depth_{\max[i]}}$$

where ($Depth_{im}$) denotes the depth of source *i* for month *m* and $Depth_{max[i]}$ the maximum observed depth for source *i*. WAI ranges from zero (no standing ground water available) to one (maximum standing water available).

Party follows

An assistant and I looked for and followed chimpanzee parties on average 20 days/month and attempted nest-to-nest follows. From May 2018–May 2019, we performed group follows and recorded APS, defined as the number of adult and subadult individuals that were seen every hour (Chapman *et al.*, 1995; Doran, 1997). For each one-hour party, we documented the number of sexually receptive females present in the party. I defined sexually receptive females as females that exhibited an anogenital swelling, regardless of the swelling size (following Wallis, 2002; van Leeuwen *et al.*, 2020b). This was because given the very recent habituation of the chimpanzees at the time, I did not have data on intra-cycle and inter-individual variation and so could not define with certainty full anogenital swellings. I assigned parties a score of 0 or 1 depending on the presence or absence of at least one swollen female. I classified habitat structure into two categories: open (comprised of woodland and swamp) and closed (riparian evergreen forest) and recorded the habitat in which the party was followed for each 1-hour scan. If a party was dispersed across the two habitat structures, I recorded the habitat in which the majority of individuals were found. Over the study period, 816 1-hour scans (for which all these variables were available) were gathered.

2.2. Data analysis

I performed all statistical analyses in R v. 3.4.0 (R Core Team, 2017) and set the significance level alpha at 0.05.

Party size model

To investigate the factors influencing APS I fit a generalized linear mixed model (GLMM; Baayen, 2008) using the function ‘glmer’ of the package ‘lme4’ (Bates *et al.*, 2015) with Poisson error structure. In this model I tested the effects of (1) FAIe, (2) the presence of swollen females, (3) habitat structure and (4) WAI, on the response variable: 1-hour-APS (n = 816). In addition, I included an interaction between FAIe and swollen females to test the influence of the presence of swollen females on APS depending on food availability. To account for seasonality in APS, I included a seasonal term as a control predictor represented by both sine and cosine of Julian date (divided by 365.25 and then multiplied by 2π; Stolwijk *et al.*, 1999; Wessling *et al.*, 2018b) to which the data correspond. This seasonal term assumes regular periodicity in a single annual cycle. I also added time of day as a control predictor to account for any potential diurnal effects on APS. I included observer identities (n = 24) as a random effect. Because consecutive scans were likely to occur under more similar social or ecological conditions, the response variable (APS) was likely to show temporal autocorrelation unexplained by the fixed effects included in the model. This may lead to a violation of the assumption of independent residuals (*i.e.*, neighboring residuals being more similar than more distant ones). Therefore, I incorporated a temporal autocorrelation term into the APS model by first running the model as described above (with all fixed and random effects included) to retrieve the residuals. I then calculated a temporal ‘autocorrelation term’ for each data point, which was the weighted mean of all other residuals, with the weight equaling the inverse number of minutes between each respective data point and the residuals (as described in *e.g.*, Furtbauer *et al.*, 2011). The weighting function followed a normal distribution. I then included the ‘autocorrelation term’ as an additional control factor into the model.

I checked for the assumptions of normally distributed and homogenous residuals by visually inspecting Q–Q plots and the residuals plotted against fitted values and found no violations. I checked for model stability by excluding each level of the random effect one at a time and comparing the estimates derived from these datasets with those derived for the full dataset and found that the model was sufficiently stable. Variance inflation factors were derived using the ‘vif’ function of the 'car' package (Fox and Weisberg, 2011) based on a standard linear model excluding the random effect and no collinearity issues were found. Before interpreting the results of the model, I first determined the significance of the full model (including all predictors and the random effect) as compared to the corresponding null model (including only the control predictors and the random effects) with a likelihood ratio test (Dobson, 2002) using the R function ‘anova’. I measured the statistical significance of each predictor using likelihood ratio tests comparing the full model with the respective reduced model (full model without the predictor). Since the interaction between FAIe and the presence of swollen females was not significant, I removed it and re-ran the model without the interaction term.

Mean absolute party size and relative party size

I first calculated annual mean for daily APS (daily mean of 1-hour-APS values), and then computed an annual mean for daily RPS (daily APS / community size (only independent individuals) × 100; Boesch, 1996). This second measure gave us a proxy for community cohesion *i.e.*, the average proportion of the community that was found together. I compared these values to other long-term study sites where these data are available.

3. Results

3.1. Predictors of absolute party size

APS showed pronounced fluctuations (mean ± SD: 6.6 ± 4.3, range: 1–19) during the study period, with a monthly minimum of 1.5 (SD = 0.7) in May 2018 and a maximum of 9.7 (SD = 3.9) in September 2018 (Figure 5.1).

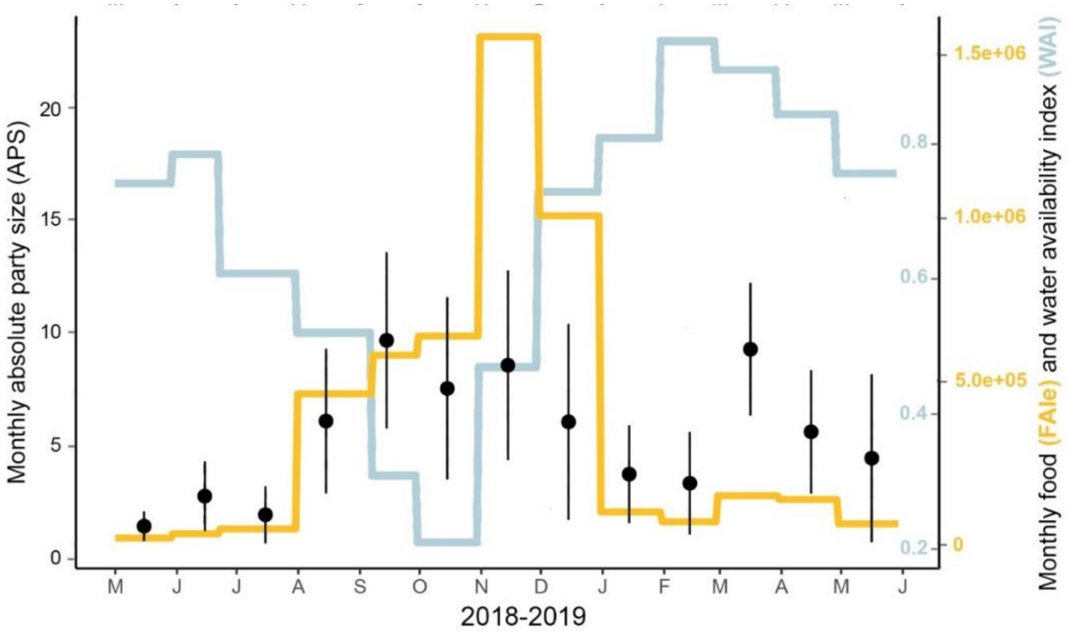


Figure 5.1 Issa chimpanzees monthly absolute party size (APS; in black), top 10 food availability index (FAIe; in yellow), water availability index (WAI; in blue) fluctuations during the study period (May 2018–May 2019). Black dots are monthly means and bars represents monthly standard deviations. APS is correlated with FAIe but not with WAI.

The APS full-null model comparison was significant (likelihood ratio test: $\chi^2 = 373.8$, df = 4, p = 2.2e-16). I found that APS significantly increased with food availability (Table 5.3, Figure 5.1) and with the presence of swollen females (Table 5.3; Figure 5.2). Moreover, I found larger parties in open habitat (Table 5.3; Figure 5.2). However, APS was not influenced by water availability (Table 5.3).

Table 5.3 GLMM testing the effect of monthly food availability index (FAIe), the presence of swollen females, habitat structure and monthly water availability index (WAI) on absolute party size (APS).

Term	Coded level	Estimate ± SE	χ2	*p*–value
(Intercept)		1.287 ± 0.068	–	–
Test predictors				
Food availability index (FAIe)[a]		**0.160 ± 0.028**	**33.890**	**5.832e-09**
Swollen females[b]	Presence	**0.571 ± 0.035**	**274.500**	**2.200e-16**
Habitat structure[b]	Open	**0.063 ± 0.030**	**4.239**	**0.039**
Water availability index (WAI)[a]		0.036 ± 0.045	0.650	0.420
Control predictors				
Temporal autocorrelation term		**0.305 ± 0.014**	**487.760**	**2.200e-16**
Cosine (Julian date)		0.032 ± 0.041	1.570	0.456[c]
Sine (Julian date)		– 0.060 ± 0.063		
Time of the day[a]		**0.824 ± 0.015**	**30.594**	**3.180e-08**

The results correspond to a reduced model not including the interaction between FAIe and swollen females (see text).
n = 816 scans. Statistically significant results ($p < 0.05$) appear in bold. Observer ID (n = 24) was included as a random factor.

[a] Z-transformed to a mean of 0 and a standard deviation of 1. Original means ± SD of the original variable: FAIe: 498,357 ± 523,197; WAI: 0.94 ± 0.35; time of the day: 394.52 ± 188.69.

[b] Estimate refers to the comparison with the reference categories: Swollen females: absence; Habitat structure: closed

[c] Indicated is the overall test of the significance of season as obtained from comparing the full model with a reduced model lacking the two terms representing season.

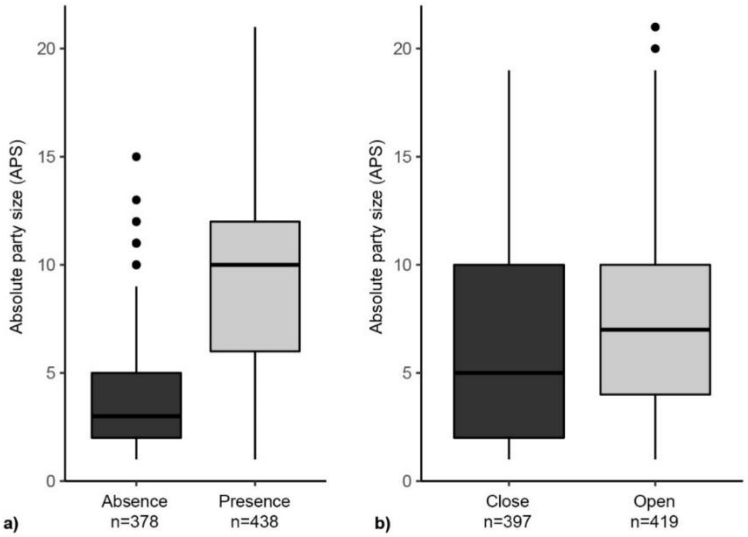


Figure 5.2 Chimpanzee absolute party size (APS) at Issa (n = 816 data points) was larger **a)** in presence of swollen females and **b)** in open habitat. Shown are medians (horizontal lines), quartiles (boxes), percentiles (2.5% and 97.5%, vertical lines)

3.2. Mean absolute party size and relative party size

Issa chimpanzee annual average of daily APS was 5.5 (SD = 3.55) which is similar to what is found in other communities (see Table 5.1) but average RPS at Issa, *i.e.*, 30.3% (SD = 19.3), was larger than the majority of the RPS values observed in other communities (see Table 5.1).

4. Discussion

In the present study, I investigated absolute and relative party size in chimpanzees from the Issa valley. This study is the first to test the impact of water availability and habitat structure on chimpanzee party size and to provide an analysis of absolute party size determinants from direct observations of an East African community at a savanna-woodland site. Additionally, by investigating relative party size at Issa, this study sheds light on two competing explanations—phylogeny and ecology—on community cohesion. Here, I compare my results with findings from other field sites and discuss the implications for hominin evolution.

4.1. Predictors of absolute party size

I found that APS varied monthly and was influenced by food availability, swollen females, and habitat structure. APS was positively correlated with food availability, with mean party size dramatically lower from May–July 2018 and again from January–February 2019 (Figure 5.1) when food availability was the lowest. Similar to chimpanzees from Kanyawara (Kibale) (Chapman *et al.*, 1995), M-group (Mahale) (Matsumoto-Oda *et al.*, 1998; Itoh and Nishida, 2007) and Taï (Boesch, 1991, 1996), Issa chimpanzees divided into small parties when food was scarce, likely to reduce intragroup feeding competition. Conversely, by reuniting when food was abundant, they were able to gain the benefits of sociality when the costs of doing so were likely minimal. In communities where food may be abundant year-round, APS is not correlated with food availability (*e.g.*, Sonso: Newton-Fisher *et al.*, 2000; Ngogo: Wakefield, 2008; Bossou: Hockings *et al.*, 2012). I could not assess whether food availability at Issa is lower (at least seasonally) than at these sites because inter-site comparisons of all feeding species productivity were not possible (due to inter-community diet differences, methodology *etc.*). However, there are some indications that food availability may be lower at Issa; for example, when looking at *Ficus* fruit, a staple, important food source for chimpanzees (Wrangham *et al.*, 1993), I noted that *Ficus* tree density at Issa was much lower (0.33 stems/ ha; unpublished data) compared to Ngogo (4.1 stems/ ha; Emery Thompson *et al.*, 2007). My results suggest that food at Issa might not be as abundant as in certain communities (*e.g.*, Ngogo) and that chimpanzees may use flexibility in their grouping patterns to adapt to the seasonal fluctuations in food availability. Future development of tools that facilitate inter-site comparisons of food productivity may shed light on the causes of population-level variability in the relationship between food availability and party size.

The presence of swollen females also had a positive effect on APS. This relationship has been described for numerous communities (see Table 5.2). Due to the very long interbirth interval that characterizes chimpanzees (*i.e.*, 5–6 years; Sugiyama, 1994; Wallis, 1997), females are sexually receptive during only 6.4% of their adult life (see Furuichi, 2006 for detailed calculation), which offers very few opportunities for males to reproduce. Because sexually receptive females are a limited resource (at Issa and elsewhere), males aggregate around them and compete for mating opportunities. Joining parties with swollen females increases copulation opportunities for males, stimulates the resumption of postpartum cycles for mothers, and initiates the first full anogenital swelling in nulliparous females (Wallis, 1992). For this reason, it is advantageous for Issa males and females to join parties with swollen females as it has been shown at other field sites (see Table 5.2). I could not define full anogenital swellings with certainty and had to consider all females that exhibited an anogenital swelling (regardless of swelling size) to be sexually receptive. However, studies at other sites revealed that males are more attracted to fully swollen females than partially swollen ones (*e.g.*, Deschner *et al.*, 2004) and parous females over nulliparous (Muller *et al.*, 2006). Also, even within the traditionally defined maximum swelling period, slight variations of swelling size occur, and male behavior closely follows these subtle changes (Deschner *et al.*, 2004). In the future, data on individual Issa female swelling patterns will allow us to refine our understanding of the relationship between female swelling size and party size at Issa. Although periodicity in the occurrence of sexual swellings within the community was beyond the scope of the present study, female swellings at Issa seem to be highly seasonal (unpublished data) and may themselves be influenced by food availability and/or diet quality as is the case in other communities (Wallis, 2002; Anderson *et al.*, 2006, Emery Thompson and Wrangham, 2008). Preliminary results at Issa (unpublished data) suggest that female sexual swellings might be positively correlated with the ingestion of leaves (and particularly young leaves of *Pterocarpus tinctorius*). Future investigation of the diet of cycling females and detailed phytochemical analysis of *P. tinctorius* (among others) may provide a better understanding of the determinants of seasonality in female reproductive ecology at Issa and, indirectly, grouping patterns and their fluctuations.

I found that habitat structure had an impact on APS with parties in open habitat being larger than those in closed habitat. This is consistent with studies on chimpanzees from Mt. Assirik (Tutin *et al.*, 1983), but also on another primate species, *i.e.*, spider monkeys from western Amazonia (Link and Di Fiore, 2013) that exhibit larger subgroup size in open habitat. Issa chimpanzees regularly travel between closed and open habitat and spend more than 50% of their time in the latter (see Chapter 4). The predators at Issa are known from both closed and open habitat. We do not have data on predators' hunting success across chimpanzee landscape at Issa and thus are unable to calculate a direct measure of predation risk. Instead, I used habitat structure as a proxy for estimating this risk with open areas considered higher risk for chimpanzees. Although woodland trees constitute temporary refuges, lower canopy connection in open habitat likely reduces escape routes for chimpanzees from predators (Stewart and Pruetz, 2013), and thus results in a landscape of fear (Coleman and Hill, 2014). The predator-avoidance hypotheses suggests that collective predator detection, defense against predators and dilution of predation risk should increase with larger subgroup size (Wrangham, 1986). Assuming that open areas are associated with higher predation risk, the results of the present study suggest that, at Issa, larger parties in open habitat might be one anti-predation strategy. This contrasts with patterns observed in the Taï forest where chimpanzees decrease APS as a response to high predation pressure (Boesch, 1991). Such difference may be due to the very dense nature of the Taï forest, which reduces early predator detection and makes large parties more conspicuous when moving through the vegetation (Boesch, 1991).

These findings provide grounds for future finer scale analyses into the spatial distribution of predation risk at Issa. For example, whilst predator relative abundance could be extracted from camera trap footage (Gerber *et al.*, 2010), future work could also assess vigilance rates and travel speed as indirect metrics of fear perception (Laundré *et al.*, 2010). Furthermore, the presence of predators inside the Issa chimpanzees' territory may vary temporally and affect chimpanzee party size inconsistently throughout the year. Subsequent studies that systematically and accurately account for spatiotemporal patterns of large carnivore presence may confirm the hypothesis of increased perceived predation risk in open habitat and resolve the role of large party sizes as an anti-predation strategy at Issa.

Similar to party size, chimpanzee party composition may vary with party location. Male chimpanzees at Bossou, for instance, are more willing to enter crop fields than females are (Hockings *et al.*, 2012) and lone or mother parties at Mt. Assirik were less frequently observed in open areas than other types of parties (Tutin *et al.*, 1983). Future investigation of Issa chimpanzee party composition with respect to habitat structure and predation risk will complement the findings on party size.

While predation risk may shape APS at Issa, risk may also come from anthropogenic sources. Humans (often accompanied by domestic dogs) are known to use the area for logging, cattle herding and poaching (Piel *et al.*, 2015). Recently, an encounter with domestic dogs resulted in the death of two Issa community members (a chimpanzee mother and her infant; Piel and Stewart, 2019). If Issa chimpanzees perceive humans (and their domestic dogs) as a threat, I would expect grouping patterns to reflect that, with larger parties near areas with the highest rates of human encounters. There are no villages within 10 km of the Issa chimpanzee home range, but there are known paths used by humans and there are seasons where humans seem to occur more frequently within the area (pers. obs.). Subsequent studies could address chimpanzee grouping patterns in response to spatiotemporal variations in human presence. An alternative explanation as to why subgroup size at Issa is greater in open areas compared to closed areas is methodological. Due to reduced visibility in closed forest, party size could have been underestimated. However, in order to minimize risk of underestimating party size, a minimum of two researchers (often placed at two extremities of the party) synchronized information on party size and composition through 2-way radios.

Finally, although water availability has been suggested to play an important role in shaping grouping patterns at sites described as savannas, such as Mt. Assirik (Tutin *et al.*, 1983) and Fongoli (Pruetz and Bertolani, 2009), it did not significantly impact APS at Issa where water remained flowing and available during the entire study period. The Senegalese sites are drier and hotter than Issa (see Chapter 2) and characterized by periods of water scarcity with only a few sparsely dispersed waterholes remaining in the late dry season (McGrew *et al.*, 1981; Pruetz, 2006), which may force chimpanzees to aggregate around these sources. Although sites with low forest cover such as Issa are always described as drier and challenging for chimpanzees in term of water acquisition, these results suggest that water may not be a scarce resource at Issa, even in the late dry season. These findings support van Leeuwen *et al.*'s (2020a) suggestion to refine our description of chimpanzee sites along with the environmental variables that characterize them rather than just assuming that savanna-woodland sites necessarily impose greater challenges (such as dehydration) than forest sites.

4.2. Community size and cohesion

Although APS showed large fluctuations and was lower on average during months of low food availability, I found that the annual mean was similar to other sites and that the Issa community was more cohesive overall (measured by mean RPS; 30.3%) compared to the majority of communities studied elsewhere (Table 5.1). High RPS was also reported at Fongoli (42.9%; Pruetz and Bertolani, 2009; or 26.0% after methodological bias correction), Taï (32.4%; Anderson *et al.*, 2002) and Bossou (52.3%; Bryson-Morrison *et al.*, 2017). Two studies conducted in M-group at Mahale (Matsumoto-Oda *et al.*, 1998; Itoh and Nishida, 2007) also revealed high mean RPS (28.9% and 47.0%; see Table 5.1) but these values resulted from the use of a method known to overestimate party size (*i.e.*, nomadic party) and were lowered when using another method (*i.e.*, 1-min scan: 12.1%, Itoh and Nishida, 2007). The present study's results provide the first evidence of increased community cohesion in an East African community and counter the hypothesis that high cohesion is specific to the western subspecies (*P. t. verus*).

Whilst average APS is roughly similar across all chimpanzee communities, demography, and especially community size, may strongly influence cohesion (Lehmann and Boesch, 2004). The communities that exhibit the highest RPS values have in common a small community size (Issa: 26, Fongoli: 35, Taï North: 31, and Bossou <20) compared to other communities (*e.g.*, Kanyawara: 55, Ngogo: 145, Sonso: 71, Mahale: 85, Table 5.1). High RPS may thus mainly be a mathematical artefact of small community size.

That notwithstanding, there are potential benefits for individuals spending more time together, independent of community size. For example, this allows for the development of very strong social bonds (through grooming for instance; Lehmann *et al.*, 2007b). Individuals that are strongly bonded can also more easily rely on each other (Dunbar, 1991; Hemelrijk and Ek, 1991; Wittig *et al.*, 2014), which may increase the effectiveness of defensive behavior against threats, either neighboring communities or predators. Among other species, crested macaques (*Macaca nigra*) and dwarf mongooses (*Helogale parvula*) for instance, individuals respond more strongly to recruitment alarm calls (*i.e.*, calls eliciting cooperative mobbing behavior) if they share strong social bonds with the caller (Micheletta *et al.*, 2012; Kern and Radford, 2016). Also, male chimpanzees prefer to patrol with partners with whom they have developed strong social bonds and on whom they can rely during agonistic intergroup encounters (Watts and Mitani, 2001). Additionally, modern humans are well known to intensify social bonds in risky situations, such as between soldiers in active warzones where relationship strength is argued to play an important role in combat effectiveness (Wong *et al.*, 2003).

Although the formation of large communities among mammals provides defense mechanisms against danger (Krause and Ruxton, 2002), a small community size may also be an efficient strategy to face threats through the facilitation of strong social bonds. Social relationships among primates require complex cognitive capacities such as individual recognition or record of previous interactions with a given partner (Barrett *et al.*, 2000) and they become exponentially demanding with increasing group size

(Dunbar and Shultz, 2007). A study on Trinidadian guppies (*Poecilia reticulata*) revealed that, under high-perceived predation risk, individuals formed smaller shoals and developed stable and more differentiated social ties, interpreted as the consequence of a conflict between forming stable social relationships and larger social groups (Heathcote *et al.*, 2017). The authors suggested that, in species where social bonds have a functional role in anti-predatory response, there is a trade-off between group size and relationship quality between group members (Heathcote *et al.*, 2017). Accordingly, the small community size (and high RPS at Issa and elsewhere) could be an advantage in defense against dangers (predators, neighboring communities, or humans), a hypothesis that needs testing. In the current study, I could not calculate predator density nor intergroup encounter rate and compare them to other sites to test whether it is higher than elsewhere, but data collected in the coming years should elucidate this question. There is only a single study that describes predator threat intensity in wild chimpanzees (Boesch, 1991) and no available data on predator density at any chimpanzee site. Issa chimpanzees are one of only two known communities that live sympatrically with leopards, lions, hyenas, and wild dogs (Tutin *et al.*, 1981; McLester *et al.*, 2016; Piel *et al.*, 2018), but whether this diverse predator guild results in greater predation pressure is unknown. Subsequent data across communities of varying sizes, predation pressure, and intergroup encounter rates may reveal an interaction of these on chimpanzee grouping behavior and especially on high cohesion in small communities.

4.3. Implications for hominin evolution

Large carnivore diversity was greater in Africa's past than it is today, and Plio-Pleistocene hominins coexisted with large predators such as *Acinonyx, Chasmaporthetes, Parahyaena, Pliocrocuta, Megantereon* and *Dinofelis* (Turner and Anton, 1997; Werdelin and Lewis, 2005). Associations of fossil hominins with remains of these carnivores indicate sympatry for millions of years (6.0–1.8 Ma) in habitats reconstructed as a mixture of woodlands and open grasslands (Cooke, 1991; Keyser, 1991; Brain, 1994; Brantingham, 1998a) and several authors have confirmed that predation was a serious threat for early hominins (*e.g.*, Treves and Naughton-Treves, 1999; Lee-Thorp *et al.*, 2000). Whilst predation has shaped human evolution (Brain, 1981; Isbell, 1994; Brantingham, 1998b), hominin anti-predator behavior remains a puzzle. Some have suggested that material culture such as fire and weaponry were the main deterrents employed to reduce predation pressure (Kortlandt, 1980; Brain, 1981). However, others have proposed that a social adaptation to high predation pressure preceded any elaboration of material culture (Treves and Palmqvist, 2007). Whilst chimpanzees are sometimes used as referential models for hominins because of their genetic and morphological similarities with humans (Cheng *et al.*, 2005), most studies to date have relied on data from 'forest-dwelling' communities, where local environmental conditions differ from the likely environment in which early hominins evolved. These conditions have important bearing on how we interpret the implications for hominins.

The present study does not dispute the pattern found at Taï, with inversely related party size and predation pressure; instead, it offers a different anti-predator scenario for what might be driving grouping patterns in chimpanzees, especially those that spend large proportions of their time in open habitat. I propose that one possible anti-predator strategy for hominins could have been to establish small, cohesive communities that form (when food availability allows) larger parties in open areas where individuals are vulnerable to terrestrial carnivore predation. This agrees with the hypothesis developed by Treves and Palmqvist (2007), who predicted that early hominin foraging parties would have adopted a more cohesive social organization with groups formed of trusted and familiar members who cooperate in anti-predator behavior. The ability to develop increasingly complex, strong, and stable social bonds in response to very high predation pressure while covering a highly heterogenous and seasonal open territory might have catalyzed hominin-chimpanzee differentiation (Grueter *et al.*, 2012; Grove and Dunbar, 2015). Derived features of human sociality such as language, intense cooperation, prosociality, and cultural transmission might have followed (Dunbar, 1996) and allowed hominins to colonize nearly all parts of the world (Grove *et al.*, 2012). This scenario remains to be tested and other studies on chimpanzees living in open environments, particularly their social strategies in the face of predators (and other sources of danger), may improve not only our understanding of the drivers of chimpanzee behavioral variability (Kalan *et al.*, 2020), but also hominin social evolution.

5. References

Alexander, R.D., 1974. The evolution of social behavior. Annual Review of Ecology, Evolution, and Systematics. 5, 325–383.

Anderson, D.P., Nordheim, E. V., Boesch, C., 2006. Environmental factors influencing the seasonality of estrus in chimpanzees. Primates. 47, 43–50.

Anderson, D.P., Nordheim, E. V., Boesch, C., Moermond, T.C., 2002. Factors influencing fission-fusion grouping in chimpanzees in the Taï National Park, Côte d'Ivoire. In: Boesch, C., Hohmann, G., Marchant, L.F. (Eds.), Behavioral Diversity in Chimpanzees and Bonobos. Cambridge University Press, Cambridge, pp. 90–101.

Aureli, F., Schaffner, C.M., Boesch, C., Bearder, S.K., Call, J., Chapman, C.A., Connor, R., Di Fore, A., Dunbar, R.I.M., Henzi, S., Holekamp, K., Korstjens, A.H., Layton, R., Lee, P., Lehmann, J., Strier, K.B., van Schaik, C.P., 2008. Fission-fusion dynamics—New research frameworks. Current Anthropology. 49, 627–654.

Baayen, R.H., 2008. Analyzing Linguistic Data: A Practical Introduction to Statistics Using R. Cambridge University Press, Cambridge.

Barrett, L., Henzi, S.P., Weingrill, T., Lycett, J.E., Hill, R.A., 2000. Female baboons do not raise the stakes but they give as good as they get. Animal Behaviour. 59, 763–770.

Basabose, A.K., 2004. Fruit availability and chimpanzee party size at Kahuzi montane forest, Democratic Republic of Congo. Primates. 45, 211–219.

Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software. 67, 1–48.

Berger, L.R., Tobias, P. V., 1996. A chimpanzee-like tibia from Sterkfontein, South Africa and its implications for the interpretation of bipedalism in *Australopithecus africanus*. Journal of Human Evolution. 30, 343–348.

Bertram, B.C.R., 1978. Living in groups: Predators and prey. In: Davies, N.B. (Ed.), Behavioural Ecology. Oxford University Press, Oxford, pp. 74–96.

Boesch, C., 1991. The effects of leopard predation on grouping patterns in forest chimpanzees. Behaviour 117, 220–242.

Boesch, C., 1996. Social grouping in Taï chimpanzees. In: McGrew, W.C., Marchant, L.F., Nishida, T. (Eds.), Great Ape Societies. Cambridge University Press, Cambridge, pp. 101–113.

Boesch, C., 2009. The Real Chimpanzee: Sex Strategies in the Forest. Cambridge University Press, Cambridge.

Boesch, C., Boesch-Achermann, H., 2000. The Chimpanzees of the Taï Forest: Behavioural Ecology and Evolution. Oxford University Press, Oxford.

Bourliere, F., Hadley, M., 1983. Present-day savannas: An overview.In: Bourliere, F. (Ed.), Ecosystems of the World, 13, Tropical savannas. Elsevier Scientific, Amsterdam, pp. 1–17.

Brain, C.K., 1981. The Hunters or the Hunted? University of Chicago Press, Chicago.

Brain, C.K., 1994. The Swartkrans palaeontological research project in perspective: Results and conclusions. South African Journal of Science. 91, 220–223.

Brantingham, P.J., 1998a. Hominid–carnivore coevolution and invasion of the predatory guild. Journal of Anthropological Archaeology. 17, 327–353.

Brantingham, P.J., 1998b. Mobility, competition, and Plio-Pleistocene hominid foraging groups. Journal of Archaeological Method and Theory. 5, 57–98.

Bryson-Morrison, N., Tzanopoulos, J., Matsuzawa, T., Humle, T., 2017. Activity and habitat use of chimpanzees (*Pan troglodytes verus*) in the anthropogenic landscape of Bossou, Guinea, West Africa. International Journal of Primatology. 38, 282–302.

Cerling, T.E., Wynn, J.G., Andanje, S.A., Bird, M.I., Korir, D.K., Levin, N.E., Mace, W., Macharia, A.N., Quade, J., Remien, C.H., 2011. Woody cover and hominin environments in the past 6 million years. Nature. 476, 51–56.

Chapais, B., 2010. The deep structure of human society: Primate origins and evolution. In: Kappeler, P.M., Silk, J. (Eds), Mind the Gap: Tracing the Origins of Human Universals. Springer-Verlag, Berlin Heidelbergpp, 19–51.

Chapman, C.A., 1990. Ecological constraints on group size in three species of neotropical primates. Folia Primatologica. 55, 1–9.

Chapman, C.A., White, F.J., Wrangham, R.W., 1993. Defining subgroup size in fission-fusion societies. Folia Primatologica. 61, 31–34.

Chapman, C.A., White, F.J., Wrangham, R.W., 1994. Party size in chimpanzees and bonobos. In: Wrangham, R.W., McGrew, W.C., de Waal, F.B.M., Heltne, P.G. (Eds.), Chimpanzee Cultures. Harvard University Press, Cambridge, pp. 41–57.

Chapman, C.A., Wrangham, R.W., Chapman, L.J., 1995. Ecological constraints on group size : An analysis of spider monkey and chimpanzee. Behavioral Ecology and Sociobiology. 36, 59–70.

Cheng, Z., Ventura, M., She, X., Khaitovich, P., Graves, T., Osoegawa, K., Church, D., DeJong, P., Wilson, R.K., Pääbo, S., Rocchi, M., Eichler, E.E., 2005. A genome-wide comparison of recent chimpanzee and human segmental duplications. Nature. 437, 88–93.

Coleman, B.T., Hill, R.A., 2014. Living in a landscape of fear: The impact of predation, resource availability and habitat structure on primate range use. Animal Behaviour. 88, 165–173.

Connor, R., Wells, R., Mann, J., Read, A., 2000. The bottlenose dolphin: Social relationships in a fission-fusion society. In: Mann, J., Connor, R.C., Tyack, P., Whitehead, H. (Eds.), Cetacean Societies: Field Studies of Whales and Dolphins. University of Chicago Press, Chicago, pp. 91–126.

Cooke, H.B.S., 1991. Dinofelis barlowi (*Mammalia, Carnivore, Felidae*) cranial material from Bolt's Farm collected by the University of California African expedition. Paleontology of Africa. 28, 9–22.

Crowther, T.W., Glick, H., Covey, K., Bettigole, C., Maynard, D., Thomas, S., Al., E., 2015. Mapping tree density at a global scale. Nature. 525, 201–205.

Davies, T.J., Daru, B.H., Bezeng, B.S., Dominique, T.C., Hempson, G.P., Kabongo, R.M., Maurin, O., Muasya, A.M., Bank, M. Van Der, Bond, W.J., 2020. Savanna tree evolutionary ages inform the reconstruction of the paleoenvironment of our hominin ancestors. Scientific Reports. 10, 1–8.

Deschner, T., Heistermann, M., Hodges, K., Boesch, C., 2003. Timing and probability of ovulation in relation to sex skin swelling in wild West African chimpanzees, *Pan troglodytes verus*. Animal

Behaviour. 66, 551–560.

Deschner, T., Heistermann, M., Hodges, K., Boesch, C., 2004. Female sexual swelling size , timing of ovulation , and male behavior in wild West African chimpanzees. Hormones and Behavior. 46, 204–215.

DeSilva, J.M., 2009. Functional morphology of the ankle and the likelihood of climbing in early hominins. Proceedings of the National Academy of Sciences. 106, 6567–6572.

Dobson, A.J., 2002. An introduction to generalized linear model. Chapman and Hall/CRC, Boca Raton.

Doran, D., 1997. Influence of seasonality on activity patterns, feeding behavior, ranging, and grouping patterns in Taï chimpanzees. International Journal of Primatology. 18, 183–206.

Dunbar, R.I.M., 1988. Primate Social Systems. Cornell University Press, London.

Dunbar, R.I.M., 1991. Functional significance of social grooming in primates. Folia Primatologica. 121–131.

Dunbar, R.I.M., 1996. Grooming, Gossip and the Evolution of Language. Harvard University Press, Cambridge.

Dunbar, R.I.M., Shultz, S., 2007. Evolution in the social brain. Science. 317, 1344–1347.

Emery Thompson, M., Kahlenberg, S.M., Gilby, I.C., Wrangham, R.W., 2007. Core area quality is associated with variance in reproductive success among female chimpanzees at Kibale National Park. Animal Behaviour. 73, 501–512.

Emery Thompson, M., Wrangham, R.W., 2008. Diet and reproductive function in wild female chimpanzees (*Pan troglodytes schweinfurthii*) at Kibale National Park, Uganda. American Journal of Physical Anthropology. 135, 171–181.

Foley, R.A., 1993. The influence of seasonality on hominid evolution. In: Ulijaszek, S.J., Strickland, S.S. (Eds.), Seasonality and Human Ecology: 35th Symposium Volume of the Society for the Study of Human Biology. Cambridge University Press, Cambridge, pp. 17–37.

Fox, J., Weisberg, S., 2011. An R Companion to Applied Regression, 2nd Edition. Sage, Thousand Oaks.

Furtbauer, I., Mundry, R., Heistermann, M., Schu, O., Ostner, J., Fu, I., 2011. You mate , I mate :

Macaque females synchronize sex not cycles. PLoS ONE. 6, 6–11.

Furuichi, T., 2006. Evolution of the social structure of hominoids—reconsideration of food distribution and the estrus sex ratio. In: Ishida, H., Tuttle, R., Pickford, M., Ogihara, N., Nakatsukasa, M. (Eds.), Human Origins and Environmental Backgrounds. Springer Science and Business Media, New York, pp. 235–248.

Furuichi, T., 2009. Factors underlying party size differences between chimpanzees and bonobos: A review and hypotheses for future study. Primates. 50, 197–209.

Gerber, B., Karpanty, S.M., Crawford, C., Kotschwar, M., Randrianantenaina, J., 2010. An assessment of carnivore relative abundance and density in the eastern rainforests of Madagascar using remotely-triggered camera traps. Oryx. 44, 219–222.

Goodall, J., 1986. The Chimpanzees of Gombe: Patterns of Behavior. The Belknap Press of Harvard University Press, Cambridge.

Grove, M., Dunbar, R.I.M, 2015. Local objects, distant symbols: Fission-fusion social systems and the evolution of human cognition. In: Coward, F., Hosfield, R., Pope, M., Wenban-Smith, F. (Eds.), Settlement, Society and Cognition in Human Evolution: Landscapes in Mind. Cambridge University Press, Cambridge, pp. 15–30.

Grove, M., Pearce, E., Dunbar, R.I.M., 2012. Fission-fusion and the evolution of hominin social systems. Journal of Human Evolution. 62, 191–200.

Grueter, C.C., Chapais, B., Zinner, D., 2012. Evolution of multilevel social systems in nonhuman primates and jumans. International Journal of Primatology. 33, 1002–1037.

Hasegawa, T., Hiraiwa-Hasegawa, M., 1983. Opportunistic and restrictive matings among wild chimpanzees in the Mahale Mountains, Tanzania. Journal of Ethology. 1, 75–85.

Hashimoto, C., Furuichi, T., Tashiro, Y., 2001. What factors affect the size of chimpanzee parties in the Kalinzu Forest, Uganda? International Journal of Primatology. 22, 947–959.

Heathcote, R.J.P., Darden, S.K., Franks, D.W., Ramnarine, I.W., Croft, D.P., 2017. Fear of predation drives stable and differentiated social relationships in guppies. Scientific Reports. 7, 1–10.

Hemelrijk, C., Ek, A., 1991. Reciprocity and interchange of grooming and ‘support’ in captive chimpanzees. Animal Behaviour. 41, 923–935.

Henschel, P., Abernethy, K.A., White, L.J.T., 2005. Leopard food habits in the Lopé National Park, Gabon, Central Africa. African Journal of Ecology. 43, 21–28.

Hockings, K.J., Anderson, J.R., Matsuzawa, T., 2012. Socioecological adaptations by chimpanzees, *Pan troglodytes verus*, inhabiting an anthropogenically impacted habitat. Animal Behaviour. 83, 801–810.

Holekamp, K.E., Cooper, S.M., Katona, C.I., Berry, N.A., Frank, L.G., Smale, L., 1997. Patterns of association among female spotted hyenas (*Crocuta crocuta*). Journal of Mammalogy. 78, 55–64.

Humle, T., Maisels, F., Oates, J.F., Plumptre, A., Williamson, E.A., 2016. *Pan troglodytes*. The IUCN Red List of Threatened Species.

Hunt, K.D., McGrew, W.C., 2002. Chimpanzees in the dry habitats of Assirik, Senegal and Semliki Wildlife Reserve, Uganda. In: Boesch, C., Hohmann, G., Marchant, L.F. (Eds.), Behavioural Diversity in Chimpanzees and Bonobos. Cambridge University Press, Cambridge, pp. 35–51.

Isbell, L.A., Young, T.P., 1996. The evolution of bipedalism in hominids and reduced group size in chimpanzees: alternative responses to decreasing resource availability. Journal of Human Evolution. 30, 389–397.

Itoh, N., Nishida, T., 2007. Chimpanzee grouping patterns and food availability in Mahale Mountains National Park, Tanzania. Primates. 48, 87–96.

Izawa, K., 1970. Unit groups of chimpanzees and their nomadism in the savanna woodland. Primates. 11, 1–45.

Kalan, A.K. *et al.*, 2020. Environmental variability supports chimpanzee behavioural diversity. Nature Communications. 11, 1–10.

Kano, T., 1971. The chimpanzee of Filabanga, western Tanzania. Primates. 12, 229–246.

Kano, T., 1982. The social group of pygmy chimpanzees (*Pan paniscus*) of Wamba. Primates 23, 171–188.

Kern, J.M., Radford, A.N., 2016. Social-bond strength influences vocally mediated recruitment to mobbing. Biology Letters. 12, 1–4.

Keyser, A.W., 1991. The palaeontology of Haasgat: A preliminary account. Paleontology of Africa. 28, 29–33.

Klein, L., Klein, D., 1971. Aspects of social behaviour in a colony of spider monkeys at San Francisco International Zoo Yearbook. 11, 175–181.

Knott, C.D., 2005. Radioimmunoassay of estrone conjugates from urine dried on filter paper. American Journal of Primatology. 67, 121–135.

Korstjens, A., Verhoeckx, I., Dunbar, R., 2006. Time as a constraint on group size in spider monkeys. Behavioral Ecology and Sociobiology. 60, 683–694.

Kortlandt, A., 1980. How might early hominins have defended themselves against large predators and food competitors? Journal of Human Evolution. 9, 79–112.

Kortlandt, A., 1983. Marginal Habitats of Chimpanzees. Journal of Human Evolution. 12, 231–278.

Krause, J., Ruxton, G.D., 2002. Living in Groups. Oxford University Press, New York.

Kummer, H., 1971. Primate Societies—Group Techniques of Ecological Adaptation. Aldine Publishing Company, Chicago.

Laundré, J.W., Hernández, L., Ripple, W.J., 2010. The landscape of fear : Ecological implications of being afraid. Open Ecology Journal. 3, 1–7.

Lee-Thorp, J., Thackeray, J.F., Van Der Merwe, N.J., 2000. The hunters and the hunted revisited. Journal of Human Evolution. 39, 565–576.

Lehmann, J., Boesch, C., 2004. To fission or to fusion: Effects of community size on wild chimpanzee (*Pan troglodytes verus*) social organisation. Behavioral Ecology and Sociobiology. 56, 207–216.

Lehmann, J., Korstjens, A.H., Dunbar, R.I.M., 2007a. Fission-fusion social systems as a strategy for coping with ecological constraints: A primate case. Evolutionary Ecology. 21, 613–634.

Lehmann, J., Korstjens, A.H., Dunbar, R.I.M., 2007b. Group size, grooming and social cohesion in primates. Animal Behaviour. 74, 1617–1629.

Lindshield, S., Hernandez-Aguilar, R.A., Korstjens, A.H., Marchant, L.F., Narat, V., Ndiaye, P.I., Ogawa, H., Piel, A.K., Pruetz, J.D., Stewart, F.A., van Leeuwen, K.L., Wessling, E.G., Yoshikawa, M., 2021. Chimpanzees (*Pan troglodytes*) in savanna landscapes. Evolutionary Anthropology

Lindshield, S.M., Danielson, B.J., Rothman, J.M., Pruetz, J.D., 2017. Feeding in fear? How adult male western chimpanzees (*Pan troglodytes verus*) adjust to predation and savanna habitat pressures. American Journal of Physical Anthropology. 1–17.

Link, A., Di Fiore, A., 2013. Effects of predation risk on the grouping patterns of white-bellied spider monkeys (*Ateles belzebuth belzebuth*) in Western Amazonia. American Journal of Physical Anthropology. 150, 579–590.

Matsumoto-Oda, A., Hosaka, K., Huffman, M.A., Kawanaka, K., 1998. Factors affecting party size in chimpanzees of the Mahale mountains. International Journal of Primatology. 19, 999–1011.

McGrew, W.C., Baldwin, P.J., Tutin, C.*E.G.*, 1981. Chimpanzees in a dry, hot and open habitat: Mt. Assirik, Senegal, West Africa. Journal of Human Evolution. 10, 227–244.

McLester, E., Stewart, F.A., Piel, A.K., 2016. Observation of an encounter between African wild dogs (*Lycaon pictus*) and a chimpanzee (*Pan troglodytes schweinfurthii*) in the Issa Valley, Tanzania. African Primates. 11, 27–36.

Micheletta, J., Waller, B.M., Panggur, M.R., Neumann, C., Duboscq, J., Agil, M., Engelhardt, A., 2012. Social bonds affect anti-predator behaviour in a tolerant species of macaque, *Macaca nigra*. Proceedings of the Royal Society B. 279, 4042–4050.

Mitani, J.C., Watts, D.P., Lwanga, J.S., 2002. Ecological and social correlates of chimpanzee party size and composition. In: Boesch, C., Hohmann, G., Marchant, L.F. (Eds.), Behavioural Diversity in Chimpanzees and Bonobos. Cambridge University Press, Cambridge, pp. 102–111.

Moore, J., 1992. Savanna chimpanzees. In: Nishida, T., McGrew, W., Marler, P., Pickford, M., de Waal, F. (Eds.), Topics in Primatology, Vol. I: Human Origins. Tokyo Press University, Tokyo, pp. 99–118.

Moore, J., 1996. Savanna chimpanzees, referential models and the last common ancestor. In: McGrew, W.C., Marchant, L.F., Nishida, T. (Eds.), Great Ape Societies. Cambridge University Press, Cambridge, pp. 275–292.

Muller, M.N., Emery Thompson, M., Wrangham, R.W., 2006. Male chimpanzees prefer mating with old females. Current Biology. 16, 2234–2238.

Nakazawa, N., Hanamura, S., Inoue, E., Nakatsukasa, M., Nakamura, M., 2013. A leopard ate a chimpanzee: first evidence from East Africa. Journal of Human Evolution. 65, 334–337.

Newton-Fisher, N.E., Reynolds, V., Plumptre, A.J., 2000. Food supply and chimpanzee (*Pan troglodytes schweinfurthii)* party size in the Budongo Forest Reserve, Uganda. International Journal of Primatology. 21, 613–628.

Nishida, T., 1968. The social group of wild chimpanzees in the Mahale Mountains. Primates 9. 167–224.

Nishida, T., 1979. The social structure of chimpanzees of the Mahale Mountains. In: McCown, E.R. (Ed.), The Great Apes. The Benjamin/Cummings Publishing Company, Menlo Park, pp. 73–121.

Nishida, T., 2012. Chimpanzees of the Lakeshore: Natural History and Culture at Mahale. Cambridge University Press, Cambridge.

Nishida, T., Takasaki, H., Takahata, Y., 1990. Demography and reproductive profiles. In: Nishida, T. (Ed.), The Chimpanzees of the Mahale Mountains. Tokyo Press University, Tokyo, pp. 63–97.

Piel, A.K., Bonnin, N., Amaya, S.R., Wondra, E., Stewart, F.A., 2018. Chimpanzees and their mammalian sympatriates in the Issa Valley, Tanzania. African Journal of Ecology. 57, 31–40.

Piel, A.K., Lenoel, A., Johnson, C., Stewart, F.A., 2015. Deterring poaching in western Tanzania: The presence of wildlife researchers. Global Ecology and Conservervation. 3, 188–199.

Piel, A.K., Stewart, F.S. 2019. Chimpanzees are being killed by poachers – researchers like us are on the frontline protecting them. The Conversation. https://theconversation.com/chimpanzees-are-being-killed-by-poachers-researchers-like-us-are-on-the-frontline-protecting-them-123699.

Piel, A.K., Strampelli, P., Greathead, E., Hernandez-aguilar, R.A., Moore, J., Stewart, F.A., 2017. The diet of savanna-woodland chimpanzees (*Pan troglodytes schweinfurthii*) at Issa, Ugalla, western Tanzania. Journal of Human Evolution. 112, 57–69.

Pokempner, A.A., 2009. Fission-fusion and foraging: Sex differences in the behavioral ecology of chimpanzees (*Pan troglodytes schweinfurthii*). Stony Brook University.

Potts, R., 2013. Hominin evolution in settings of strong environmental variability. Quaternary Science Reviews. 73, 1–13.

Potts, K.B., Lwanga, J.S., 2014. Floristic heterogeneity at Ngogo, Kibale National Park, Uganda and possible implications for habitat use by chimpanzees (*Pan troglodytes*). African Journal of Ecology. 52, 427–437.

Prang, T.C., Ramirez, K., Grabowski, M., Williams, S.A., 2021. Ardipithecus hand provides evidence that humans and chimpanzees evolved from an ancestor with suspensory adaptations. Science Advances. 7, 1–14.

Pruetz, J.D., 2006. Feeding ecology of savanna chimpanzees. In: Hohmann, G., Robbins, M.M., Boesch, C. (Eds.), Feeding Ecology in Apes and Other Primates. Cambridge University Press, Cambridge, pp. 161–182.

Pruetz, J.D., Bertolani, P., 2009. Chimpanzee (*Pan troglodytes verus*) behavioral responses to stresses associated with living in a savannah-mosaic environment: Implications for hominin adaptations to open habitats. PaleoAnthropology. 252–262.

Pruetz, J.D., Fulton, S.J., Marchant, L.F., McGrew, W.C., Schiel, M., Waller, M., 2008. Arboreal nesting as anti-predator adaptation by savanna chimpanzees (*Pan troglodytes verus*) in Southeastern Sénégal. American Journal of Primatology. 70, 393–401.

Pruetz, J.D., Herzog, N.M., 2017. Savanna chimpanzees at Fongoli, Senegal, navigate a fire landscape. Current Anthropology 58, 337–349.

Pruetz, J.D., Kante, D., 2010. Successful return of a wild infant chimpanzee (*Pan troglodytes verus*) to its natal group after capture by poachers. African Primates. 7, 35–41.

Reed, K.E., Fish, J.L., 2005. Tropical and temperate seasonal influences on human evolution. In: Brockman, D. K., van Schaik, C. P. (Eds.), Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates.Cambridge University Press, Cambridge, pp. 491–520.

Robinson, J.R., Rowan, J., Campisano, C.J., Wynn, J.G., Reed, K.E., 2017. Late Pliocene environmental change during the transition from *Australopithecus* to *Homo*. Nature Ecology and Evolution. 1, 1–7.

Sakura, O., 1994. Factors affecting party size and composition of chimpanzees (*Pan troglodytes verus*) Bossou, Guinea. International Journal of Primatology. 15, 167–183.

Samuni, L., Mielke, A., Preis, A., 2020. Intergroup competition enhances chimpanzee (*Pan troglodytes verus*) in-group cohesion. International Journal of Primatology. 41, 342–362.

Sayers, K., Lovejoy, C.O., 2008. The chimpanzee has no clothes. Current Anthropology 49, 87–114.

Schulke, O., Ostner, J., 2012. Ecological and social influences on sociality. In: Mitani, J., Call, J. (Eds.), The Evolution of Primate Societies. University of Chicago Press, Chicago, pp. 195–219.

Sommer, V., Adanu, J., Faucher, I., Fowler, A., 2004. Nigerian chimpanzees (*Pan troglodytes vellerosus*) at Gashaka: Two years of habituation efforts. Folia Primatologica. 75, 295–316.

Stewart, F.A., Pruetz, J.D., 2013. Do chimpanzee nests serve an anti-predatory function? American Journal of Primatology. 75, 593–604.

Stolwijk, A.M., Straatman, H., Zielhuis, G.A., 1999. Studying seasonality by using sine and cosine functions in regression analysis. Journal of Epidemiology and Community Health. 53, 235–238.

Sueur, C., King, A.J., Conradt, L., Kerth, G., Lusseau, D., Mettke-Hofmann, C., Schaffner, C.M., Williams, L., Zinner, D., Aureli, F., 2011. Collective decision-making and fission-fusion dynamics: A conceptual framework. Oikos. 120, 1608–1617.

Sugiyama, Y., 1968. Social organization of chimpanzees in the Budongo Forest, Uganda. Primates. 9, 225–258.

Sugiyama, Y., 1994. Age-specific rate and lifetime reproductive success of chimpanzees at Bossou, Guinea. American Journal of Primatology. 32, 311–318.

Suzuki, A., 1969. An ecological study of chimpanzees in a savanna woodland. Primates. 10, 103–148.

Terborgh, J., Janson, C.H., 1986. The socioecology of primate groups. Annual Review of Ecology, Evolution, and Systematics. 17, 111–135.

Treves, A., Naughton-Treves, L., 1999. Risk and opportunity for humans coexisting with large carnivores. Journal of Human Evolution. 36, 275–282.

Treves, A., Palmqvist, P., 2007. Reconstructing hominin interactions with mammalian carnivores. In: Gurskey-doyen, S.L., Nekaris, A.K.I. (Eds.), Primate Anti-Predator Strategies. Springer Science and Business Media, New York, pp. 355–381.

Tsukahara, T., 1993. Lions eat chimpanzees: The first evidence of predation by lions on wild chimpanzees. American Journal of Primatology. 29, 1–11.

Turner, A., Anton, M., 1997. The Big Cats and their Fossil Relatives. Columbia University Press, New York.

Tutin, C.E.G., McGinnis, P., 1981. Chimpanzee reproduction in the wild. In: Graham, C. (Ed.), Reproductive Biology of the Great Apes. New York Academic Press, New York, pp. 239–64.

Tutin, C.E.G., McGrew, W.C., Baldwin, P.J., 1981. Responses of wild chimpanzees to potential predators. In: Chiarelli, A.B., Corruccini, R.S. (Eds.), Primate Behavior and Sociobiology. Springer Verlag, Berlin, pp. 136–141.

Tutin, C.E.G., McGrew, W.C., Baldwin, P.J., 1983. Social organization of savanna-dwelling chimpanzees, *Pan troglodytes verus*, at Mt. Assirik, Sénégal. Primates. 24, 154–173.

van Leeuwen, K.L., Hill, R.A., Korstjens, A.H., 2020a. Classifying chimpanzee (*Pan troglodytes*) landscapes across large-scale environmental gradients in Africa. International Journal of Primatology. 41, 800–821.

van Leeuwen, K.L., Matsuzawa, T., Sterck, E.H.M., Koops, K., 2020b. How to measure chimpanzee party size? A methodological comparison. Primates. 61, 201–212.

van Schaik, C.P., 2016. Social evolution in hominins. In: Cartmill, M., Brown, K. (Eds.), The Primate Origins of Human Nature. John Wiley & Sons, Hoboken, pp. 299–313.

van Schaik, C.P., Hörstermann, M., 1994. Predation risk and the number of adult males in a primate group: a comparative test. Behavioral Ecology and Sociobiology. 35, 261–272.

Villioth, J., 2018. The foraging ecology of two neighbouring chimpanzee communities from Budongo Forest. University of Kent.

Wakefield, M.L., 2008. Grouping patterns and competition among female *Pan troglodytes schweinfurthii* at Ngogo, Kibale National Park, Uganda. International Journal of Primatology. 29, 907–929.

Wallis, J., 1992. Socioenvironmental effects on timing of first postpartum cycles in chimpanzees. In: Nishida, T., McGrew, W.C., Marler, P., Pickford, M., de Waal, F. (Eds.), Topics in Primatology, Vol. 1: Human Origins. University of Tokyo Press, Tokyo, pp. 119–130.

Wallis, J., 1997. A survey of reproductive parameters in the free-ranging chimpanzees of Gombe National Park. Journal of Reproduction and Fertility. 109, 297–307.

Wallis, J., 2002. Seasonal aspects of reproduction and sexual behavior in two chimpanzee populations: A comparison of Gombe (Tanzania) and Budongo (Uganda). In: Boesch, C., Hohmann, G., Marchant, L.F. (Eds.), Behavioural Diversity in Chimpanzees and Bonobos. Cambridge University Press, Cambridge, pp. 181–191.

Watts, D.P., Mitani, J.C., 2001. Boundary patrols and intergroup encounters in wild chimpanzees. Behaviour. 138, 299–327.

Werdelin, L., Lewis, M.E., 2005. Plio-Pleistocene Carnivora of eastern Africa: Species richness and turnover patterns. Zoological Journal of the Linnean Society. 144, 121–144.

Wessling, E.G., Deschner, T., Mundry, R., Pruetz, J.D., Wittig, R.M., Kühl, H.S., 2018a. Seasonal variation in physiology challenges the notion of Chimpanzees (*Pan troglodytes verus*) as a forest-adapted species. Frontiers in Ecology and Evolution. 6, 1–21.

Wessling, E.G., Dieguez, P., Llana, M., Pacheco, L., Pruetz, J.D., Kühl, H.S., 2020. Chimpanzee (*Pan troglodytes verus*) density and environmental gradients at their biogeographical range edge. International Journal of Primatology. 41, 822–848.

Wessling, E.G., Kühl, H.S., Mundry, R., Deschner, T., Pruetz, J.D., 2018b. The costs of living at the edge: Seasonal stress in wild savanna-dwelling chimpanzees. Journal of Human Evolution. 121, 1–11.

Willems, E.P., Hill, R.A., 2009. Predator-specific landscapes of fear and resource distribution : Effects on spatial range use. Ecology. 90, 546–555.

Wilson, M.L., 2001. Imbalances of power: How chimpanzees respond to the threat of intergroup aggression. Harvard University.

Wilson, M.L., Boesch, C., Fruth, B., Furuichi, T., Gilby, I.C., Hashimoto, C., Hobaiter, C.L., Hohmann, G., Itoh, N., Koops, K., Lloyd, J.N., Matsuzawa, T., Mitani, J.C., Mjungu, D.C., Morgan, D., Muller, M.N., Mundry, R., Nakamura, M., Pruetz, J., Pusey, A.E., Riedel, J., Sanz, C., Schel, A.M., Simmons, N., Waller, M., Watts, D.P., White, F., Wittig, R.M., Zuberbühler, K., Wrangham, R.W., 2014. Lethal aggression in *Pan* is better explained by adaptive strategies than human impacts. Nature. 513, 414–417.

Wittemyer, G., Douglas-Hamilton, I., Getz, W.M., 2005. The socioecology of elephants: Analysis of the processes creating multitiered social structures. Animal Behaviour. 69, 1357–1371.

Wittig, R.M., Crockford, C., Langergraber, K.E., Zuberbu, K., Wittig, R.M., Crockford, C., 2014. Triadic social interactions operate across time: A field experiment with wild chimpanzees. Proceedings of the Royal Society. 281, 1–9.

Wittiger, L., Boesch, C., 2013. Female gregariousness in western chimpanzees (*Pan troglodytes verus*) is influenced by resource aggregation and the number of females in estrus. Behavioral Ecology and Sociobiology. 67, 1097–1111.

Wong, L., Kolditz, T.A., Millen, R.A., Potter, T.M., 2003. Why they fight: Combat motivation in the Iraq war. DTIC Document.

Wrangham, R.W., 1986. Ecology and social relationship in two species of chimpanzee. In: Rubenstein, D.I., Wrangham, R.W. (Eds.), Ecological Aspects of Social Evolution. Princeton University Press, Princeton, pp. 352–378.

Wrangham, R.W., 1987. Evolution of social structure. In: Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W., Struhsaker, T.T. (Eds.), Primate Societies. University of Chicago Press, Chicago , pp. 282–296.

Wrangham, R.W., Conklin, N.L., Etot, G., Obua, J., Hunt, K.D., Hauser, M.D., Clark, A.P., 1993. The value of figs to chimpanzees. International Journal of Primatology. 14, 243–256.

Yamakoshi, G., 2004. Food seasonality and socioecology in *Pan*: Are west African chimpanzees another bonobo? Afr. Study Monogr. 25, 45–60.

Zuberbühler, K., Jenny, D., 2002. Leopard predation and primate evolution. Journal of Human Evolution. 43, 873–88.

Chapter 6: General discussion and future directions

1. Thesis summary and findings overview

Despite nearly six decades of field research across more than twenty communities, gaps remain in our knowledge of chimpanzees, particularly when it comes to communities inhabiting savanna-woodlands, the ecological edge of the species range. Studies of chimpanzees in these dry habitats have the potential to reveal new behavioral and ecological diversity across the species. Savanna-woodlands differ from forests in having significantly less rainfall, which is strongly seasonal, as well as lower plant density and diversity, all of which result in important fluctuations in resource availability. This study investigated the feeding, ranging, and grouping responses of eastern chimpanzees (*Pan troglodytes schweinfurthii*) to temporal fluctuations of resource (food and water) availability in a savanna-woodland environment. I also compared results with published data from other chimpanzee populations. This work contributes to the understanding of the relationships between environment and behavior for this species and furthermore, is useful to the paleoanthropological scientific community who could build on these results to address scenarios in human evolution.

Chapter 2 provided specific details of the study site, study subjects, the general methods of data collection, and described Issa environmental data. I confirmed that rainfall at Issa was highly seasonal as well as food and water availability during the study period. Inter-site comparisons suggested that Issa is as dry, open, and seasonal but not as hot as other savanna-woodland sites.

Chapter 3 examined Issa chimpanzee diet and its temporal variation throughout the year. I showed that, similar to what is found in other savanna-woodland communities, Issa chimpanzees consumed fewer plant species than chimpanzees from more forested sites. Like elsewhere, Issa chimpanzees consumed mostly fruit, but other items such as leaves, flowers, and termites were also important in their annual diet, probably because they provide higher protein contents. The most consumed item in Issa chimpanzee diet was figs and contrary to some other communities it was not a fallback food (FBF) but a preferred food. When preferred foods were scarce, Issa chimpanzees consumed young leaves from tree species growing in woodlands.

Chapter 4 looked at Issa chimpanzee ranging patterns and influences on temporal variation throughout the year. Home range was larger than most other communities for which data are available. Home range changed monthly and, in contrast to previous reports from other chimpanzee communities, I found that during periods of low food availability chimpanzees increased their daily path length. Water availability, however, did not influence daily path length. Neither food nor water availability influenced habitat use.

Chapter 5 explored Issa chimpanzee grouping patterns and their determinants. Compared to other communities, the Issa community was highly cohesive. I found that absolute party size at Issa was positively correlated with food availability and was higher in open areas, which are potentially characterized by a high predation risk

2. Implications

Most data gathered on chimpanzee behavioral ecology come from forested sites and early studies have attempted to derive the species general behavior based only on communities living in this habitat. We now know that different ecological pressures can lead to within-species variation in behavior (Kalan *et al.*, 2020). To date, some studies have been conducted on the behavioral ecology of chimpanzees living in savanna-woodlands (reviewed in Marchant *et al.*, 2020 and in Lindshield *et al.*, 2021), but these have predominantly relied on indirect sampling methods (but see work at Fongoli). By focusing on a chimpanzee community living in an understudied biome, the current study improves our understanding of the relationship between environment and behavior for this species, and particularly of the behavioral responses to extreme fluctuations in resource availability. Moreover, it addresses a significant gap in our knowledge of the dietary ecology, ranging and grouping patterns of chimpanzees in a savanna-woodland ecosystem by providing data from direct behavioral follows.

Evidence from chapter 2 indicates that chimpanzees at Issa experience important seasonal fluctuations in food and water availability and probably lower environmental productivity and botanical diversity than at more forested sites. Chimpanzees at Issa, and other savanna-woodland populations, likely face increased challenges, and more specifically in term of resource acquisition (Kano, 1971; Baldwin *et al.*, 1982; Moore, 1992; Pruetz and Bertolani, 2009) potentially requiring additional adaptations to safeguard their survival (Kalan *et al.*, 2020, Lindshield *et al.,* 2021). A lower dietary breadth, preference for figs, flowers and termites and a seasonal reliance on young leaves demonstrate some of the ways in which Issa chimpanzee diet diverge from those in more forested sites and may serve as a strategy to face increase food scarcity. Regarding Issa ranging patterns, yearly home range at Issa was larger than at forested sites probably because the lower tree density and diversity of savanna-woodlands require chimpanzees to cover a larger area to find enough food to maintain their dietary requirements (Kano, 1971; Baldwin *et al.*, 1982; Moore, 1992; Pruetz and Bertolani, 2009). Issa chimpanzees responded to seasonal variation in food availability by switching their home range and adjusting their daily path length. However, habitat use was more likely to be influenced by seasonal events such as (anthropogenic and/ or natural) annual fire than by food availability. Chimpanzees were also flexible to adjust their grouping patterns by reducing their party size during periods of low food availability, likely to lower feeding competition during these challenging periods. Moreover, Issa chimpanzee sociality seemed to be influenced by habitat, with larger parties in open habitat, possibly as an anti-predation strategy. This contrasts with results from Taï forest (Boesch, 1991), in the only study that examined chimpanzee party size responses to predation risk. This latter result offers a different anti-predator behavior scenario for what might be driving grouping patterns in chimpanzees, especially those that spend large proportions of their time in open habitat, and consequently highlights the importance of studying chimpanzees in different environmental conditions. Community size at Issa was lower compared to other communities, likely because it was restricted by the lower plant productivity and diversity (Wessling *et al.*, 2020). One consequence of the reduced community size is an increased cohesion (Lehmann and Boesch, 2004), which could be advantageous to limit predation risk (Micheletta *et al.*, 2012; Kern and Radford, 2016). Finally, contrary to hypotheses that have been drawn at other sites (*e.g.*, Baldwin *et al.*, 1982), water availability at Issa did not have an impact neither on grouping nor on ranging patterns. These findings highlight inter-site variability of savanna-woodlands and challenge the assumption that these landscapes necessarily impose greater water scarcity challenges than forest sites (*e.g.*, Lindshield *et al.*, 2021).

Combined, these results emphasize chimpanzee behavioral variation and species adaptation to a wide variety of landscapes including food-scarce, highly seasonal, and open savanna-woodlands. Following Strier (2017), behavioral variation is defined as differences in behavioral patterns observed in populations, groups, and individuals of the same species and are thought to result from various factors such as genetic differences, and responses to local conditions. Numerous examples of behavioral variation exist across primates with, for instance, diet, activity budgets, group size, and social structure varying between populations (*e.g.*, Ménard and Vallet, 1997; Chapman and Rothman, 2009; Potts *et al.*, 2011). These differences reflect the extent of behavioral variation within a species, but they do not automatically imply behavioral flexibility. Flexibility is defined as the behavioral responses to an external constraint (such as food scarcity) and that theoretically return to their original form after the constraint stops (Kappeler *et al.*, 2013). In the case of Issa chimpanzees, behavioral variation would correspond to the narrower diet, larger home range, smaller community and increased cohesion compared to other communities, whereas the behavioral modifications in response to food scarcity (such as reliance on leaves, reduced party size, home range shift and daily path length increase) would represent the behavioral flexibility of this population. These mechanisms allow the chimpanzee species to live across a wide range of habitats from evergreen forests to savanna-woodlands and to successfully cope with spatiotemporal variations in environmental variables (such a food availability) by promoting behaviors that are adapted to their environment. In that sense, a recent study elegantly demonstrated that seasonal and unstable environmental conditions may act as an external force favoring within-species behavioral diversification (Kalan *et al.*, 2020).

Such behavioral diversity is not restricted to chimpanzees but is found in many other species, with one of the best examples being humans, who have colonized nearly all parts of the world (Roberts and Stewart, 2018). Some authors hypothesized that this is precisely early hominins exceptional behavioral flexibility in response to increasing environmental variability that may have differentiated humans from chimpanzees and allowed the former to thrive at the expense of others (Reed, 1997; Potts, 1998; deMenocal, 2004). Since behavior does not fossilize and is difficult to reconstruct for extinct species, a comparative approach using extant primates for modelling early hominins behavior can facilitate empirical research on human evolution (Mitani, 2013; Plavcan, 2013). If we postulate that early hominins had some similarities with present-day chimpanzees, and especially those that live in savanna-woodlands, then this indicates that, likewise, they may have used a diverse toolbox of behaviors to adapt and survive to the constraints of their environment.

Transitions from closed, wet rainforests to more open and arid landscapes during the Plio-Pleistocene (Reed, 1997; deMenocal, 2004) are predicted to have largely influenced hominin diet. These new landscapes were likely characterized by climate unpredictability as well as more patchily distributed resources in both the temporal and spatial scale (Foley, 1993; Reed and Fish, 2005). Early hominins may have thus been faced with the challenge of maintaining dietary quality, particularly during periods of food scarcity (Ulijaszek *et al.*, 2013). Diet diversification and the development of innovative ways of acquiring alternative or novel foods may have been key behavioral adaptations that allowed hominins to survive and thrive in these landscapes (Wrangham *et al.*, 2009; Nelson and Hamilton, 2017; Lüdecke *et al.*, 2018). Whereas Issa chimpanzees, for instance, fallback on young leaves during the lean season, early hominins dentitions exhibit little evidence for shearing, which suggests that leaves would not have been their FBF (Teaford and Ungar, 2000). Their thick enamel (especially in *Paranthropus*, Grine and Martin, 1988) suggests instead a shift away from leaves toward an increased consumption of underground storage organs (USOs) (Laden and Wrangham, 2005). Some authors hypothesized that hominins were obligated to shift to USOs when moving into open savanna-woodlands because these landscapes would have insufficient leaves and herbs to sustain populations of large primates (Laden and Wrangham, 2005). The finding that Issa chimpanzees rely on the consumption of young leaves growing in the open woodlands during the food-scarce season does not support this assumption. It rather suggests that hominins choice for USOs may have had another justification than simply the absence of leaves. USOs primary function is to store nutrients (mainly energy supplying nutrients such as carbohydrates) for the plant to survive unfavorable conditions (Hladik *et al.*, 1984) and may have had sufficient nutritional qualities (probably more than leaves) to be significant FBF for early hominins (Conklin-Brittain *et al.*, 2002; Laden and Wrangham, 2005; Wrangham *et al.*, 2009). Hominins probably developed innovative techniques and digging tools that allowed them to efficiently and rapidly extract USOs in sufficient quantities to fulfill their energy requirements (Brain and Shipman, 1993; D'Errico and Backwell, 2009). Some authors (Hernandez-Aguilar *et al.*, 2007; Motes-rodrigo *et al.*, 2019) suggested that chimpanzees may also be capable of using tools to extract USOs (although direct observations on wild individuals have yet to be recorded) but hominins possibly innovated with a higher frequency of excavation, diversity, efficiency and quality of tools than their hominid counterparts.

Transitions to more open landscapes are also predicted to have influenced hominin ranging patterns (Copeland *et al.*, 2011). As the Plio-Pleistocene landscapes dried, resources were less abundant and more widely distributed (deMenocal, 2004), which would have required individuals to travel farther to harvest the same amount of food (Isbell and Young, 1996). The findings that Issa chimpanzees have a larger home range than most of the chimpanzee populations living in forests and that their daily path length was negatively correlated with food availability support this hypothesis. Similarly, some authors hypothesized that hominins movements would have been influenced by the availabity of temporary and scattered water courses (Baldwin *et al.*, 1982; Speth, 1987; Finlayson, 2013), but the results of the current study could not confirm this assumption. The need to maintain resource intake (either food or water) as they were becoming more widely separated could have favored the evolution of bipedalism (Isbell and Young, 1996). Hominins' bipedal locomotion, by decreasing energy expenditure, was likely a more efficient way for covering long distance (Rodman and Mehenry, 1980; Isbell and Young, 1996, Pontzer, 2017) thus easing the colonization of dry, seasonal and resource-scarce landscapes.

Finally, early hominin sociality is also suspected to have been greatly impacted during the expansion in savanna-woodlands (Grove and Dunbar, 2015; van Schaik, 2016) although reconstruction of hominins social life is still a very debated topic. In this study, I found that Issa chimpanzees had a smaller community size than the majority of communities elsewhere. Because savanna-woodlands are scarcer in resources, there may be more competition between individuals resulting in a smaller carrying capacity than other landscapes (Wessling *et al.*, 2020). To date we have no paleontological evidence for the mean hominin population size, but we can hypothesize that, similarly to Issa chimpanzees, lower population sizes and/or lower population densities may have been one of the early hominins' adaptations to savanna-woodlands (Aureli *et al.*, 2008; Foley and Gamble, 2009). I hypothesize that smaller communities may also have the advantage of promoting higher social cohesion, trust and familiarity among members that would be beneficial in predator detection and defense (Treves and Palmqvist, 2007), especially in open areas where predation risk may be increased due to the lack of escape routes (Stewart and Pruetz, 2013). Furthermore, savanna-woodlands environments are likely to have selected for a greater degree of fissioning behavior in feeding parties (Potts, 1998; Grove *et al.*, 2012) especially during food-scarce seasons, which may have been one of the bases for later human complex social structure (Foley, 2001).

In sum, moving from closed, wet rainforests to more open and arid savanna-woodlands was a driver for behavioral diversification in early hominins and likely led to some key characteristics of the hominin lineage such as bipedalism, a large brain, tool use and manufacture, cooperative defense and hunting, and complex socio-cultural abilities (Foley, 1995; Potts, 1998; Antón *et al.*, 2014; Roberts and Stewart, 2018). One assumption that emerges from the present work is that, although chimpanzees give us insights in human adaptations to savanna-woodlands, hominins may not have responded in the same way to the pressures associated with these landscapes as did their hominid counterparts (Brockman and van Schaik, 2005). Although chimpanzees are capable of living across a wide range of habitats, including savanna-woodlands (van Leeuwen *et al.*, 2020; Lindshield *et al.*, 2021), and exhibit behavioral flexibility to cope with seasonal fluctuations in resource availability (Kalan *et al.*, 2020), hominins probably took advantages of these challenges to come up with some novel, competitive and more efficient behavioral strategies (Foley, 1993; Potts, 1998). This likely framed the evolution and expansion of the human species at the expense of other primates. Studying chimpanzees living in Plio-Pleistocene-like landscapes allow us to understand better the pressures that were acting on early hominins, to infer their possible behavioral responses to these challenges and test them against paleontological records, to determine what may have differentiated human and *Pan* lineages as well as providing new directions for future research.

3. Limitations and future research perspectives

In this section, I address the limitations of this thesis and propose research perspectives for future work at Issa and elsewhere.

Interannual variations

Long-term research has validated that chimpanzee diet, grouping, and ranging behavior demonstrate considerable interannual variation within communities (*e.g.*, Lehmann and Boesch, 2004; Watts, 2012; Nakamura *et al.*, 2013). A recognizable limitation of this study is its length since drawing conclusions about Issa chimpanzees' behavior from twelve months of data is, by necessity, limited in scope. Issa chimpanzees' habituation is recent, and this study was the first to systematically document Issa chimpanzee behavior from direct observations and follows. Ongoing research at Issa continues to monitor diet, ranging and grouping patterns and may reveal interannual variations in these behaviors.

Food availability calculation

Some limitations are associated with the calculation of the food availability index. I calculated FAIe based on phenological data collected every month, which probably did not capture all temporal fluctuations on food availability. Future research at Issa could be more specific, especially for studies that have a focus on seasonality, and use a finer temporal scale (*e.g.*, bimonthly). Additionally, individuals from the same plant species may be particularly patchily distributed and/or may fruit asynchronously (*e.g.*, fig species), and the trees monitored during our phenological sampling may have not accurately capture these spatiotemporal variations within Issa large home range. An increase in the number of individuals sampled for these particular species as well as a finer spatial scale (*e.g.*, focusing on areas where the chimpanzees are foraging at that particular time of year) would help to resolve this problem. An attempt should also be done to identify individual *Ficus* species to alleviate the effect of potential asynchrony between the different *Ficus* species that have all been grouped into a single category for this study. Furthermore, among the most important thirteen plant species in Issa chimpanzees' diet during the study period, three species were not recorded on phenological trails (namely *Englerophytum magalismontanum, Landolphia owariensis* and *Syzygium guineense)* because these trails were established before obtaining dietary data from direct feeding observations. Future studies at Issa should include these species in the phenological record to get a more precise estimation of the annual variation in important foods availability. Additionally, termites were the fourth most important item in Issa chimpanzee annual diet, however, due to time constraints I could not include their availability in the calculation of the food availability index which may have thus underestimated FAIe when termites were available. Subsequent studies could calculate termite mounds density at Issa and estimate monthly termite availability/accessibility for chimpanzees in order to include these values in the calculation of FAIe.

Water availability calculation

The water availability index I used in this study is based on global water availability in Issa range, *i.e.*, the average of water availability at eight different locations, and does not take into account the variability between these locations. Variability in water availability across Issa range could affect chimpanzee behavior and particularly their ranging patterns. Efforts could be done in the future to include variability in the water availability index. Future studies at Issa could, as well, precisely document water availability, particularly during the driest months, by walking along Issa rivers and recording the permanent pools and water holes.

Nutrition

This study focused on recording qualitatively Issa chimpanzee diet, food choice and nutrient intake, but subsequent studies could focus on determining quantitatively the nutrients and energy gained daily by Issa chimpanzees as well as exploring temporal and individual variations. This could be achieved by coupling counts of the number of units eaten for each feeding item during full day focal follows with macronutrient analyses (Rothman *et al.*, 2011) and would allow to calculate a foraging (*i.e.*, searching, handling, extracting) time *versus* energy and nutrient gain ratio for each food and thus better comprehend Issa chimpanzees feeding decisions.

Sex differences

In this study, I did not examine sex-related differences in behavior, however several studies have revealed that female chimpanzees' patterns of diet, ranging, and grouping differ from those of males. Females are expected to maximize energetic and nutritional intake due to the high costs of reproduction (Key and Ross, 1999). Sex differences in foraging have been observed in other populations, with a male bias in meat consumption (Gilby *et al.*, 2017), but a female bias in termite fishing (Lonsdorf, 2005) and nut pounding (Boesch and Boesch, 1981). Chimpanzee females have been observed to be generally less gregarious, to stay closer to core areas of their home range, and to travel less than males (Wrangham and Smuts, 1980; Murray *et al.*, 2006; Emery Thompson *et al.*, 2007). During the study period, I gathered more data from males than from females (primarily because males are generally noisier, more gregarious, less shy, and thus easier to find and follow). I included a sex effect in my models but did not analyze male and female differences in diet and grouping patterns due to a general lack in data points. Consequently, some of the behavioral patterns observed here may have been male-biased and future research could examine sex-related behavioral differences at Issa and particularly their respective responses to fluctuations in resource availability.

Physiological analyses

A detailed examination of Issa chimpanzee physiological status and its seasonal fluctuations was originally planned for this project. I collected urine and fecal samples for C-peptide, creatinine, and glucocorticoid analyses in order to assess nutritional and dehydration stress through the year (Emery Thompson and Knott, 2008; Wessling *et al.*, 2018). I could collect an appropriate number of samples every month that would have allowed these analyses. Unfortunately, this work could not be completed due to sample transportation problems and Covid-19 related delays in laboratory analyses. The achievement of such a study in the future could allow a better evaluation of the impact of fluctuations in resources availability on Issa chimpanzees physiology, as well as a better understanding of the behavioral strategies that mitigate these pressures (Wessling *et al.*, 2018).

Predation

Predation is a major selective force that affects many primate species, including large-bodied chimpanzees (Isbell, 1994; Zuberbühler and Jenny, 2002; Laundré *et al.*, 2010; Coleman and Hill, 2014). Issa chimpanzees live with four potential predators: lions, leopards, hyenas and wild dogs (Piel *et al.*, 2018), and the results of this study highlight that predation may have an impact on both grouping and ranging patterns. In this study, I used a proxy for spatial variation in predation risk and was not able to assess temporal variations. Consequently, predation risk estimation was likely underestimated and future fine scale analyses into the spatiotemporal distribution of predation risk and predation pressure at Issa could allow refinement of the current findings and shed light on the factors explaining seasonal variations of Issa chimpanzees ranging and grouping patterns. Camera trap footage would allow to assess spatiotemporal variation in predator density (Gerber *et al.*, 2010) while behavioral record of chimpanzee vigilance level and travel speed could be used as indirect metrics for spatial variation in risk perception (Laundré *et al.*, 2010).

Inter-site comparison and method standardization

We still have much to learn about the ecological and behavioral diversity of the chimpanzee species. Future studies should continue to explore chimpanzee behavior at new sites with diverse environmental challenges. Unfortunately, one major limitation of this study was the difficulty in comparing results with those of other communities. For instance, I could not compare general food availability at Issa with those of other sites due to differences in methodology, species availability and diet choices between populations. Uniformization of methods to estimate crucial values such as food availability index, party size, home range size, *etc.*, would facilitate inter-site comparison and may allow to better tackle the role of environmental variability in explaining chimpanzee behavioral diversity, as well as continuing to shed light on the pressures that may have shaped human evolution and contributed to the differentiation between human and chimpanzee lineage.

4. References

Antón, S.C., Potts, R., Aiello, L.C., 2014. Evolution of early Homo : An integrated biological perspective. Science. 345, 45–59.

Aureli, F., Schaffner, C.M., Boesch, C., Bearder, S.K., Call, J., Chapman, C.A., Connor, R., Di Fore, A., Dunbar, R.I.M., Henzi, S., Holekamp, K., Korstjens, A.H., Layton, R., Lee, P., Lehmann, J., Strier, K.B., van Schaik, C.P., 2008. Fission-fusion dynamics - New research frameworks. Current Anthropology. 49, 627–654.

Baldwin, P.J., McGrew, W.C., Tutin, C.E.G., 1982. Wide-ranging chimpanzees at Mt. Assirik, Senegal. International Journal of Primatology. 3, 367–385.

Boesch, C., 1991. The effects of leopard predation on grouping patterns in forest chimpanzees. Behaviour. 117, 220–242.

Boesch, C., Boesch, H., 1981. Sex differences in the use of natural hammers by wild chimpanzees: A preliminary report. Journal of Human Evolution. 10, 585–593.

Brain, C.K., Shipman, P., 1993. The Swartkrans bone tools. Swartkrans: a cave's chronicle of early man. Transvaal Museum Monograph. 8, 195–215.

Brockman, D.K., van Schaik, C.P., 2005. Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates. Cambridge University Press, Cambridge.

Chapman, C.A., Rothman, J.M., 2009. Within-species differences in primate social structure : evolution of plasticity and phylogenetic constraints. Primates. 50, 12–22.

Coleman, B.T., Hill, R.A., 2014. Living in a landscape of fear: The impact of predation, resource availability and habitat structure on primate range use. Animal Behaviour. 88, 165–173.

Conklin-Brittain, N.L., Wrangham, R.W., Smith, C.C., 2002. A two-stage model of increased dietary quality in early hominid evolution: the role of fiber. In: Ungar, P.S., Teaford, M.F. (Eds.), Human Diet: Its Origin and Evolution. Bergin and Garvey, Westport, pp. 61–76.

Copeland, S.R., Sponheimer, M., De Ruiter, D.J., Lee-Thorp, J.A., Codron, D., Le Roux, P.J., Grimes, V., Richards, M.P., 2011. Strontium isotope evidence for landscape use by early hominins. Nature. 474,

76–78.

D’Errico, F., Backwell, L., 2009. Assessing the function of early hominin bone tools. Journal of Archaeological Science. 36, 1764–1773.

deMenocal, P.B., 2004. African climate change and faunal evolution during the Pliocene-Pleistocene. Earth and Planetary Science Letters. 220, 3–24.

Emery Thompson, M., Kahlenberg, S.M., Gilby, I.C., Wrangham, R.W., 2007. Core area quality is associated with variance in reproductive success among female chimpanzees at Kibale National Park. Animal Behaviour. 73, 501–512.

Emery Thompson, M., Knott, C.D., 2008. Urinary C-peptide of insulin as a non-invasive marker of energy balance in wild orangutans. Hormones and Behavior. 53, 526–535.

Finlayson, C., 2013. The water optimisation hypothesis and the human occupation of the mid-latitude belt in the Pleistocene. Quaternary International. 300, 22–31.

Foley, R.A., 1993. The influence of seasonality on hominid evolution. In: Ulijaszek, S.J., Strickland, S.S. (Eds.), Seasonality and Human Ecology: 35th Symposium Volume of the Society for the Study of Human Biology. Cambridge University Press, Cambridge, pp. 17–37.

Foley, R.A., 1995. The adaptive legacy of human evolution: A search for the environment of evolutionary adaptedness. Evolutionary Anthropology: Issues, News, and Reviews. 4, 194–203.

Foley, R.A., 2001. Evolutionary perspectives on the origins of human social institutions. Proceedings of the British Academy. 110, 171–195.

Foley, R.A., Gamble, C., 2009. The ecology of social transitions in human evolution. Philosophical Transactions of the Royal Society B: Biological Sciences. 364, 3267–3279.

Gerber, B., Karpanty, S.M., Crawford, C., Kotschwar, M., Randrianantenaina, J., 2010. An assessment of carnivore relative abundance and density in the eastern rainforests of Madagascar using remotely-triggered camera traps. Oryx. 44, 219–222.

Gilby, I.C., Machanda, Z.P., Malley, R.C.O., Murray, C.M., Lonsdorf, E. V, Walker, K., Mjungu, D.C., Otali, E., Muller, M.N., Emery, M., Pusey, A.E., Wrangham, R.W., 2017. Predation by female chimpanzees: Toward an understanding of sex differences in meat acquisition in the last common ancestor of Pan and Homo. Journal of Human Evolution. 110, 82–94.

Grine, F.E., Martin, L.B., 1988. Enamel thickness and development in *Australopithecus* and *Paranthropus*. In: Grine, F.E. (Ed.), Evolutionary History of the '"Robust"' Australopithecines. Aldine de Gruyter, New York, pp. 3–42.

Grove, M., Dunbar, R., 2015. Local objects, distant symbols: Fission-fusion social systems and the evolution of human cognition. In: Coward, F., Hosfield, R., Pope, M., Wenban-Smith, F. (Eds.), Settlement, Society and Cognition in Human Evolution: Landscapes in Mind. Cambridge University Press, Cambridge, pp. 15–30.

Grove, M., Pearce, E., Dunbar, R.I.M., 2012. Fission-fusion and the evolution of hominin social systems. Journal of Human Evolution. 62, 191–200.

Hernandez-Aguilar, R.A., Moore, J., Pickering, T.R., 2007. Savanna chimpanzees use tools to harvest the underground storage organs of plants. Proceedings of the National Academy of Sciences. 104, 19210–19213.

Hladik, A., Bahuchet, S., Ducatillion, C., Hladik, C.M., 1984. The tuberous plants of the central African rain-forest. Revue d'Ecologie (la Terre et la Vie). 39, 249–290.

Isbell, L.A., 1994. Predation on primates: ecological patterns and evolutionary consequences. Evolutionary Anthropology. 3, 61–71.

Isbell, L.A., Young, T.P., 1996. The evolution of bipedalism in hominids and reduced group size in chimpanzees: alternative responses to decreasing resource availability. Journal of Human Evolution. 30, 389–397.

Kalan, A.K., Kulik, L., Arandjelovic, M., Boesch, C., Haas, F., Dieguez, P., Barratt, C.D., Abwe, E.E., Agbor, A., Angedakin, S., Aubert, F., Ayimisin, E.A., Bailey, E., Bessone, M., Brazzola, G., Buh, V.E., Chancellor, R., Cohen, H., Coupland, C., Curran, B., Danquah, E., Deschner, T., Dowd, D., Eno-Nku, M., Michael Fay, J., Goedmakers, A., Granjon, A.C., Head, J., Hedwig, D., Hermans, V., Jeffery, K.J., Jones, S., Junker, J., Kadam, P., Kambi, M., Kienast, I., Kujirakwinja, D., Langergraber, K.E., Lapuente, J., Larson, B., Lee, K.C., Leinert, V., Llana, M., Marrocoli, S., Meier, A.C., Morgan, B., Morgan, D., Neil, E., Nicholl, S., Normand, E., Ormsby, L.J., Pacheco, L., Piel, A., Preece, J., Robbins, M.M., Rundus, A., Sanz, C., Sommer, V., Stewart, F., Tagg, N., Tennie, C., Vergnes, V., Welsh, A., Wessling, *E.G.*, Willie, J., Wittig, R.M., Yuh, Y.G., Zuberbühler, K., Kühl, H.S., 2020. Environmental variability supports chimpanzee behavioural diversity. Nature Communications. 11, 1–10.

Kano, T., 1971. The chimpanzee of Filabanga, western Tanzania. Primates. 12, 229–246.

Kappeler, P.M., Barrett, L., Blumstein, D.T., Clutton-Brock, T.H., Kappeler, P.M., 2013. Constraints and flexibility in mammalian social behaviour : introduction and synthesis. Philosophical Transactions of the Royal Society B. 368, 3–10.

Kern, J.M., Radford, A.N., 2016. Social-bond strength influences vocally mediated recruitment to mobbing. Biology letters. 12, 1–9.

Key, C., Ross, C., 1999. Sex differences in energy expenditure in non-human primates. Proceedings of the Royal Society B. 266, 2479–2485.

Laden, G., Wrangham, R., 2005. The rise of the hominids as an adaptive shift in fallback foods: Plant underground storage organs (USOs) and australopith origins. Journal of Human Evolution. 49, 482–498.

Laundré, J.W., Hernández, L., Ripple, W.J., 2010. The landscape of fear : Ecological implications of being afraid. The Open Ecology Journal. 3, 1–7.

Lehmann, J., Boesch, C., 2004. To fission or to fusion: Effect of community size on wild chimpanzee (*Pan troglodytes versus*) social organisation. Behavioral Ecology and Sociobiology. 56, 207–216.

Lindshield, S., Hernandez-Aguilar, R.A., Korstjens, A.H., Marchant, L.F., Narat, V., Ndiaye, P.I., Ogawa, H., Piel, A.K., Pruetz, J.D., Stewart, F.A., van Leeuwen, K.L., Wessling, E.G., Yoshikawa, M., 2021. Chimpanzees (*Pan troglodytes*) in savanna landscapes. Evolutionary Anthropology

Lonsdorf, E. V, 2005. Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park, Tanzania. Animal Behaviour Monographs. 70, 673–683.

Lüdecke, T., Kullmer, O., Wacker, U., Sandrock, O., Fiebig, J., Schrenk, F., Mulch, A., 2018. Dietary versatility of Early Pleistocene hominins. Proceedings of the National Academy of Sciences of the United States of America. 115, 13330–13335.

Marchant, L.F., Wessling, E.G., Lindshield, S.M., 2020. Introduction to the special issue on savanna chimpanzees. International Journal of Primatology. 41, 767–774.

Ménard, N., Vallet, D., 1997. Behavioral responses of barbary macaques (*Macaca sylvanus*) to variations in environmental conditions in Algeria. American Journal of Primatology. 304, 285–304.

Micheletta, J., Waller, B.M., Panggur, M.R., Neumann, C., Duboscq, J., Agil, M., Engelhardt, A., 2012. Social bonds affect anti-predator behaviour in a tolerant species of macaque, *Macaca nigra*. Proceedings of the Royal Society B: Biological Sciences. 279, 4042–4050.

Mitani, J.C., 2013. Chimpanzee models of human behavioral evolution. In: Sponheimer, M., Lee-Thorp, J.A., Reed, K.E., Ungar, P.S. (Eds.), Early Hominin Paleoecology. University Press of Colorado, Boulder, pp. 397–435.

Moore, J., 1992. Savanna chimpanzees. In: Nishida, T., McGrew, W.C., Marler, P., Pickford, M., de Waal, F.B.M. (Eds.), Topics in Primatology, Vol. I: Human Origins. Tokyo Press University, Tokyo, pp. 99–118.

Moore, J., 1996. Savanna chimpanzees, referential models and the last common ancestor. In: McGrew, W.C., Marchant, L.F., Nishida, T. (Eds.), Great Ape Societies. Cambridge University Press, Cambridge, pp. 275–292.

Motes-rodrigo, A., Majlesi, P., Pickering, T.R., Id, M.L., Axelsen, H., Minchin, T.C., Tennie, C., Hernandez-Aguilar, A.R., 2019. Chimpanzee extractive foraging with excavating tools : Experimental modeling of the origins of human technology. PLoS ONE. 14, 1–23.

Murray, C.M., Eberly, L., Pusey, A.E., 2006. Foraging strategies as a function of season and rank among wild female chimpanzees (*Pan troglodytes*). Behavioral Ecology. 32, 1020–1028.

Nakamura, M., Corp, N., Fujimoto, M., Fujita, S., Hanamura, S., Hayaki, H., Hosaka, K., Huffman, M.A., Inaba, A., Inoue, E., Itoh, N., Kutsukake, N., Kiyono-Fuse, M., Kooriyama, T., Marchant, L.F., Matsumoto-Oda, A., Matsusaka, T., McGrew, W.C., Mitani, J.C., Nishie, H., Norikoshi, K., Sakamaki, T., Shimada, M., Turner, L.A., Wakibara, J. V., Zamma, K., 2013. Ranging behavior of Mahale chimpanzees: A 16 year study. Primates. 54, 171–182.

Nelson, S. V, Hamilton, M.I., 2017. Evolution of the human dietary niche. Initial transitions. In: Muller, M.N., Wrangham, R.W., Pilbeam, D. (Eds.), Chimpanzees and Human Evolution. Harvard University Press, Cambridge, pp. 311–338.

Piel, A.K., Bonnin, N., Amaya, S.R., Wondra, E., Stewart, F.A., 2018. Chimpanzees and their mammalian sympatriates in the Issa Valley, Tanzania. African Journal of Ecology. 57, 31–40.

Plavcan, J.M., 2013. Reconstructing social behavior from fossil evidence. In: Begun, D.R. (Ed.), A Companion to Paleoanthropology. Blackwell Publishing, Chichester, pp. 226–243.

Pontzer, H., 2017. Economy and endurance in human evolution. Current Biology. 27, 613–621.

Potts, K.B., Watts, D.P., Wrangham, R.W., 2011. Comparative feeding ecology of two communities of chimpanzees (*Pan troglodytes*) in Kibale National Park, Uganda. International Journal of Primatology. 32, 669–690.

Potts, R., 1998. Environmental hypotheses of hominin evolution. American Journal of Physical Anthropology. 107, 93–136.

Pruetz, J.D., Bertolani, P., 2009. Chimpanzee (*Pan troglodytes verus*) behavioral responses to stresses associated with living in a savannah-mosaic environment: Implications for hominin adaptations to open habitats. PaleoAnthropology. 252–262.

Reed, K.E., 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. Journal of Human Evolution. 32, 289–322.

Reed, K.E., Fish, J.L., 2005. Tropical and temperate seasonal influences on human evolution. In: Brockman, D.K., van Schaik, C.P. (Eds.), Seasonality in Primates: Studies of Living and Extinct

Human and Non-Human Primates. Cambridge University Press, Cambridge, pp. 491–520.

Roberts, P., Stewart, B.A., 2018. Defining the 'generalist specialist' niche for Pleistocene Homo sapiens. Nature Human Behaviour. 2, 542–550.

Rodman, P.S., Mehenry, H.M., 1980. Bioenergetics and the origin of hominid bipedalism. American Journal of Physical Anthropology. 52, 103–106.

Rothman, J.M., Chapman, C.A., Soest, P.J. Van, 2011. Methods in primate nutritional ecology: A user's guide. International Journal of Primatology. 33, 542–566.

Speth, J.D., 1987. Early hominid subsistence strategies in seasonal habitats. Journal of Archaeological Science. 14, 13–29.

Stewart, F.A., Pruetz, J.D., 2013. Do chimpanzee nests serve an anti-predatory function? American Journal of Primatology. 75, 593–604.

Strier, K.B., 2017. What does variation in primate behavior mean? American Journal of Physical Anthropology. 162, 4–14.

Teaford, M.F., Ungar, P.S., 2000. Diet and the evolution of the earliest human ancestors. PNAS. 97, 13506–13511.

Treves, A., Palmqvist, P., 2007. Reconstructing hominin interactions with mammalian carnivores. In: Gurskey-doyen, S.L., Nekaris, A.K.I. (Eds.), Primate Anti-Predator Strategies. Springer Science+Business Media, New York, pp. 355–381.

Ulijaszek, S., Mann, N., Elton, S., Ulijaszek, S., Mann, N., Elton, S., 2013. Seasonality of environment and diet. In: Ulijaszek, S., Mann, N., Elton, S. (Eds.), Evolving Human Nutrition. Cambridge University Press, Cambridge, pp. 83–116.

van Leeuwen, K.L., Hill, R.A., Korstjens, A.H., 2020. Classifying chimpanzee (*Pan troglodytes*) landscapes across large-scale environmental gradients in Africa. International Journal of Primatology. 41, 800–821.

van Schaik, C.P., 2016. Social evolution in hominins. In: Cartmill, M., Brown, K. (Eds.), The Primate Origins of Human Nature. John Wiley & Sons, Hoboken, pp. 299–313.

Watts, David P, 2012. Long-term research on chimpanzee behavioral ecology in Kibale National Park, Uganda. In: Kappeler, P.M., Watts, D P (Eds.), Long-Term Field Studies of Primates. Berlin, Heidelberg, pp. 313–338.

Wessling, E.G., Dieguez, P., Llana, M., Pacheco, L., Pruetz, J.D., Kühl, H.S., 2020. Chimpanzee (*Pan troglodytes verus*) density and environmental gradients at their biogeographical range edge. International Journal of Primatology. 41, 822–848.

Wessling, E.G., Kühl, H.S., Mundry, R., Deschner, T., Pruetz, J.D., 2018. The costs of living at the edge : Seasonal stress in wild savanna-dwelling chimpanzees. Journal of Human Evolution. 121, 1–11.

Wrangham, R., Cheney, D., Seyfarth, R., Sarmiento, E., 2009. Shallow-water habitats as sources of fallback foods for hominins. American Journal of Physical Anthropology. 140, 630–642.

Wrangham, R.W., Smuts, B.B., 1980. Sex differences in the behavioural ecology of chimpanzees in the Gombe National Park, Tanzania. Journal of reproduction and fertility. 28, 13–31.

Zuberbühler, K., Jenny, D., 2002. Leopard predation and primate evolution. Journal of Human Evolution. 43, 873–886.